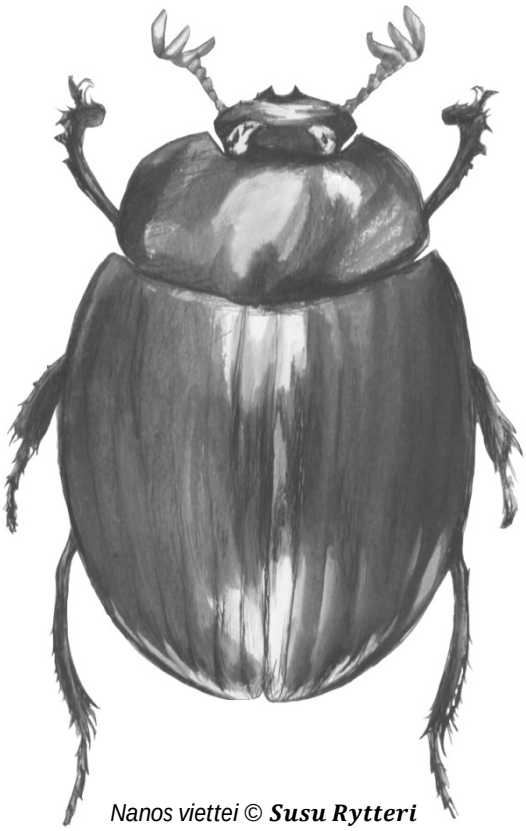
Dung beetle communities in degraded rainforest landscapes in Madagascar



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Torppa Kaisa Anneli

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Tiivistelmä – Referat – Abstract

The purpose of this thesis was to examine the diversity and species composition of dung beetle (Scarabaeinae) communities in degraded rainforest landscapes in southeastern Madagascar. Several studies elsewhere in the world have revealed that forest-dwelling dung beetle communities and especially large species suffer from forest degradation and fragmentation by decreased species diversity. The most important factors affecting community structure of forest-dwelling dung beetles are habitat area, connectivity and vegetation quality i.e. microclimate. The hypothesis of this study was that the situation is the same in Madagascar. As dung beetles provide several important ecosystem services, like nutrient cycling and bioturbation, loss of dung beetle diversity imposes a secondary threat to the extraordinary nature of Madagascar by decreasing the regeneration ability of vegetation.

Material for the study was collected in forest fragments of different size and quality between two areas of primary tropical rainforest – Ranomafana National Park and Vatovavy mountain – in November and December 2011 and January 2012. The sampling was conducted by transects of 30–60 fish- or carrion-baited pitfall traps which were set up in 55 localities in the study area. In each locality, several variables were measured to describe the vegetation and microclimatic conditions. The variables included temperature, humidity, estimate of vegetation quality by 6 observation-based classes, vegetation density, hights of three clearly visible vegetation layers, altitude and slope steepness. In addition, connectivities were measured for the localities using GIS and a satellite image –based vegetation classification. In order to demonstrate the differences between certain localities the study sites were divided into seven zones in terms of their distance from the Ranomafana National Park, average connectivity of the transects and elevation.

Altogether 4,199 individuals belonging to 24 species were collected. Six of the species are currently under identification process in the Paris Museum of Natural History. According to the preliminary results they include two species new to science. Largest numbers of species were collected from good quality fragments between Ranomafana and Vatovavy. Also, a clear transition zone in species composition was detected a few kilometers west from Vatovavy, where altitude changes sharply.

The study reveals that the species assemblages in the forest fragments and degraded forest areas are surprisingly species rich. This may, however, be partly because of extinction debt, and many of the still surviving species may soon die out due to restricted dispersal possibilities. Connectivity and vegetation quality were shown to have an effect on Canthonini species richness, with less species in less connected areas and lower vegetation quality. Vegetation quality was also shown to have an impact on the proportions of species with different body length: more small and medium-sized (< 8 mm) species were found in fragments where vegetation was more degraded.

In addition to revealing how rainforest fragmentation and degradation affect local communities, the study gives interesting information about the distribution of certain species of *Epilissus* (Scarabaeinae: Canthonini). It has been known before that four species of *Epilissus* show elevational differentiation in their occurrence in Ranomafana. In this study, two more species of the same genus, *E. prasinus* and *E. emmae obscurpennis*, were shown to continue this pattern in lower elevations near Vatovavy mountain, about 50 kilometers east of Ranomafana.

Avainsanat – Nyckelord – Keywords
Scarabaeinae, biodiversity, habitat fragmentation, primary forest, secondary forest

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Tiivistelmä – Referat – Abstract

Tämän tutkielman tavoitteena oli selvittää sademetsien pirstoutumisen ja laadun heikentymisen vaikutuksia paikallisiin lantakuoriaisyhteisöihin (Scarabaeinae) Kaakkois-Madagaskarissa. Useissa muissa aihetta käsittelevissä tutkimuksissa muualla maailmassa on selvinnyt, että metsien lantakuoriaisyhteisöt kärsivät metsien pirstoutumisesta ja laadun heikentymisestä. Lajiston monimuotoisuus vähenee ja erityisesti suuret lajit väistyvät. Tärkeimpiä lajistoon vaikuttavia tekijöitä ovat olleet elinympäristön pinta-ala, kytkeytyneisyys sekä kasvillisuuden laatu ja mikroilmasto. Tämän tutkimuksen hypoteesina oli, että tilanne olisi sama myös Madagaskarilla. Koska suurten lantakuoriaisten on osoitettu olevan ekologisilta vaikutuksiltaan erityisen merkittäviä esimerkiksi ravinteiden kierron, maaperän ilmastoimisen ja siementen kuljetuksen takia, niiden häviäminen saattaa entisestään heikentää Madagaskarin viimeisten metsien uusiutumiskykyä.

Tutkimusaineisto kerättiin erikokoisissa ja -laatuisissa metsäsaarekkeissa kahden yhtenäisen sademetsäalueen, Ranomafanan kansallispuiston ja Vatovavy-vuoren, välillä marraskuussa ja joulukussa 2011 sekä tammikuussa 2012. Näytteet kerättiin kala- tai kanasyötillä varustettujen kuoppapyydysten avulla 55 eri pisteestä. Jokaiseen pisteeseen asetettiin 30-60 pyydyksen linja. Pyydysten asettamisen lisäksi jokaisessa pisteessä mitattiin alueen kasvillisuuden laatua ja mikroilmastoa indikoivia muuttujia, kuten lämpötila ja ilmankosteus, kasvillisuuden laadun arviointi 6 luokkaisella asteikolla, puuston tiheys, kolmen selkeästi erottuvan kasvillisuuskerroksen korkeudet, rinteen kaltevuus sekä korkeus merenpinnasta. Lisäksi jokaiselle pisteelle laskettiin paikkatieto-ohjelma ArcGIS:n ja kasvillisuusluokituksen avulla kytkeytyneisyys. Alueiden välisten erojan havainnollistamiseksi tutkimuspisteet jaettiin seitsemään eri alueeseen saarekkeiden kytkeytyneisyyden, etäisyyden Ranomafanan kansallispuistosta ja sekä korkeuden merenpinnasta perusteella.

Aineiston keruussa pyydystettiin yhteensä 4 199 yksilöä 24 eri lajista. Kuusi näistä lajeista on edelleen määritettävänä Pariisin luonnontieteellisessä museossa, mutta alustavien päätelmien mukaan lajeista kaksi olisi tieteelle uusia. Eniten lajeja kerättiin hyvälaatuisista metsäsaarekkeista Ranomafanan ja Vatovavyn väliltä. Ranomafanan ja Vatovavyn alueiden lajistot poikkeavat huomattavasti toisistaan, ja lajiston vaihettumisvyöhyke paikannettiin muutaman kilometrin päähän Vatovavysta länteen, jossa korkeus muuttuu erityisen jyrkästi.

Tutkielman mukaan huonolaatuisissa ja eristyneissäkin saarekkeissa on yllättävän monimuotoinen lajisto. Tämä saattaa tosin johtua osittain sukupuuttovelasta (engl. extinction debt), ja moni näistä vielä nykyään elävistä lajeista saattaa pian kuolla sukupuuttoon heikkojen levittäytymismahdolli-suuksia vuoksi. Kytkeytyneisyydellä ja kasvillisuuden laadulla on yhteys Canthonini-sukuryhmän lantakuoriaisten lajirunsauteen siten, että eristyneissä ja huonolaatuisissa saarekkeissa on vähemmän lajeja. Kasvillisuuden laadulla on vaikutusta myös erikokoisten lajien runsauteen: huonolaatuisissa saarekkeissa suurempi osa lantakuoriaisista kuuluu pienikokoisiin (< 8 mm) lajeihin.

Metsien pirstoutumisen ja laadun heikentymisen vaikutusten lisäksi tutkimuksessa havaittiin mielenkiintoinen ilmiö tiettyjen *Epilissus*–suvun (Scarabaeinae: Canthonini) lajien levinneisyydessä. Kuten jo aikaisemmin on osoitettu, neljä *Epilissus*–lajia esiintyy Ranomafanan alueella siten, että kaksi lajia esiintyy korkeammalla meren pinnasta ja kaksi matalammalla. Tämän tutkimuksen perusteella havaittiin, että sama kaava jatkuu myös alemmilla korkeuksilla Ranomafanasta itään. Kaksi saman suvun lajia, *E. prasinus* ja *E. emmae obscurpennis* esiintyivät pääasiassa alle 400 metrin korkeudessa Vatovavyn alueella.

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Scarabaeinae, monimuotoisuus, pirstoutuminen, elinympäristön laatu, primäärinen metsä, sekundäärinen metsä

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1 Introduction

1.1 Background

More than half of the species on Earth are estimated to live in tropical rainforests (e.g. Gardner et al. 2010). Tropical rainforests are mostly located in the poorest countries in the developing world, where the human population is growing fast. More land is needed for agriculture and other purposes, and even though deforestation of rainforests has been slightly slowing down, the area of primary rainforest is still lost by about 1% per year (FAO 2010). In addition to the reduction in area, human-induced changes in forest quality and connectivity impose a great threat to the survival of species (Hanski 2005). Increasing numbers of species that have evolved to inhabit continuous primary rainforests are forced to live in fragments of primary forest, secondary forests of different successional stages, various kinds of tree plantations and more open habitats, such as pastures and farmlands. It is likely that many species that have adapted to continuous forests have non-viable populations in the fragmented and degraded forest landscapes. In any case, it is important to learn more about the dynamics of species inhabiting human-modified forest landscapes (Diaz et al. 2010).

Madagascar is one of the global priority areas for conservation due to the great pressure of deforestation on the unique flora and fauna of the island (Myers et al. 2000). During its 165 million years of isolation from the mainland Africa and 80 million years of isolation from the Indian plate (Rakotosamimanana 2003), Madagascar has gained an exceptionally high degree of endemism: approximately half of the breeding bird species (Hawkins & Goodman 2003) and more than 90% of other vertebrates (excluding the still poorly known fishes) are endemic in Madagascar (Goodman et al. 2003, Raxworthy 2003). In non-marine invertebrates, the degree of endemism has been estimated to be 86% (Goodman & Benstead 2005). Among the subject of this thesis, dung beetles (Scarabaeinae and Aphodiinae), 96% of the species are endemic (Miraldo et al. 2011).

Most of the remaining closed forests in Madagascar are humid evergreen forests at different elevations along the eastern mountain chain. In addition, there are seasonally dry deciduous forests in the west and dry deciduous forests in the south (du Puy & Moat 1996). Approximately

90% of all animal species in Madagascar, including almost all of the endemic Malagasy dung beetles, are confined to forests, whose area has been rapidly decreasing. It has been estimated that by 2000, only 16% of the original forest cover remained, and additionally there have been dramatic losses in forest quality and connectivity (Harper et al. 2007). Forest loss seemed to slow down in 1990's, but it has recently started to increase again, probably reflecting the political instability in the country (Allnutt et al. 2013).

Fragmentation of tropical wet forests and the effect of agriculture on biodiversity have been much studied during the past decades. However, the research has been mostly focused on plants, mammals and birds, and there is relatively little knowledge about the effects of forest modification on insects and other invertebrates (Nichols et al. 2007). Dung beetles (Scarabaeinae) have become one of the more popular study organisms to fill this gap in knowledge, but research has so far been conducted in a limited number of locations, mostly in Latin America and South-Eastern Asia (Spector 2006, Nichols et al. 2007, Slade et al. 2007). During the past decade, Malagasy dung beetles have been intensively studied by researchers and students from the University of Helsinki (e.g. Viljanen 2009, Wirta et al. 2010, Miraldo et al. 2011, Välitalo 2012). As the taxonomy, ecology and biogeography of Malagasy dung beetles are now relatively well known, they offer an opportunity to study the responses of these species to rainforest destruction and fragmentation.

1.2 Fragmentation and degradation of tropical rainforests

Species suffer from the loss of rainforest directly due to the diminished area of suitable habitat, but there are also other changes that affect the viability of species and populations. In particular, the spatial distribution of the remaining fragments of habitat across the landscape has a big influence on the long-term persistence of many species (Hanski 1999). Gradual degradation of forests furthermore changes many forest features especially in the areas of most intensive modification but also within forest remnants due to increasing edge effects, including access by people and non-forest species, erosion, wind and so forth (Saunders et al. 1991, Murcia 1995). Finally, changes in the species composition may have unpredictable secondary effects on the rest of the community (van der Putten et al. 2004) and the functionality of the ecosystem (Didham et al. 1996, Lewis 2009).

The persistence of a population depends on the balance between not only birth and death rates but in many cases also on the balance between emigration and immigration. In many species, populations are naturally structured into groups of interacting local populations, but habitat destruction and fragmentation makes dispersal among local populations even more consequential. In an increasing number of cases, the landscape-level survival of species depends on the ability of individuals to disperse among widely scattered pieces of suitable habitat in the landscape. The degree to which this happens depends on several factors, including the number and areas of available habitat patches, distances between them, dispersal abilities of the species and the type of the matrix habitat between the patches (Hanski 1999).

In addition to changes in the spatial distribution of remaining forest, loss of vegetation has a great impact on the quality of the remaining habitat and the capacity of the area to recover from forest loss. Vegetation influences local climatic conditions and it stabilizes the water cycle. Removing vegetation increases temperature fluctuations between day and night, and it may cause erosion as soil becomes more directly exposed to rainfall, wind and radiation (Saunders et al. 1991). Constant physical stress especially at forest edges may lead to changes in the species composition of forest fragments, as the original forest species are not well adapted to such conditions (Murcia 1995). The effects on one species may have significant and often unpredictable consequences for many others through complex interactions between the trophic levels (van der Putten et al. 2004).

Many responses to habitat destruction are highly species specific, but nonetheless some general patterns have emerged. The species that suffer the most of forest degradation are usually highly specialized, poor dispersers and breed slow, while many species with the opposite traits may profit of landscape modification (McKinney & Lockwood 1999). This is true for example for most invasive species which have often been concluded to accelerate the rate of extinction of native species (Didham et al. 2005). As many species with strict habitat requirements are replaced by more generalist species, habitat modification tends to generate species poor and homogeneous communities (McKinney & Lockwood 1999). In many cases, such perturbed communities are dominated by one or a few species, and the functional significance of the less abundant ones is small (Hillebrandt et al. 2008).

The above-mentioned general consequences of forest degradation and fragmentation apply also to forest-dwelling dung beetles as will be discussed in Section 2. Rainforest destruction and

fragmentation cause reduction in species diversity, especially of large and functionally important species, with most drastic effects where forest has been completely cleared (Nichols et al. 2007, Slade et al. 2010, Barragán et al. 2011). Secondary forests and tree plantations maintain some of the diversity, depending on the characteristics of the local species (Nichols et al. 2007). In addition to loss of species, also the evenness of the species composition is typically reduced, and in many studies the most degraded forests have been dominated by a few small-bodied species (Nichols et al. 2007). This is an important finding, as it has been observed that small species are not able to compensate the functionality of larger species in nutrient cycling, secondary seed dispersal and bioturbation (Slade et al. 2007, Slade et al. 2010, Barragán et al. 2011). It is possible that the capacity of the forest to recover will be reduced by the reduction in ecosystem functions provided by large-bodied dung beetles (Nichols et al. 2008).

1.3 Malagasy dung beetles

The term *dung beetle* refers to three subfamilies in the family Scarabaeidae (scarab beetles). These subfamilies are Aphodiinae, Geotrupinae and Scarabaeinae. The family Scarabaeidae is included in the superfamily Scarabaeoidea (Hanski & Cambefort 1991, 22). The subfamilies Aphodiinae and Geotrupinae are scarce in the tropics (Hallfter & Matthews 1966, 3), and I will only deal with the subfamily Scarabaeinae in this thesis. There are about 260 known genera and about 6000 species of Scarabaeinae in the world (ScarabNet taxon database 2013).

The oldest dung beetle (Scarabaeinae) fossils have been found in France and Switzerland and have been estimated to be 40 million years old. However, it is possible that there were dung beetles as early as at the end of the Mesozoic Era, 65 million years ago. After that, during the Cenozoic Era, global forest cover was reduced and forests were partly replaced by savannas and grasslands. At that time the rapid radiation of mammals started, which is assumed to have facilitated the radiation of dung beetles (Hanski & Cambefort 1991). Especially the evolution of ungulates and other big herbivores can be assumed to have strongly increased dung beetle diversity. Subsequently dung beetles spread from open savannas also to forested habitats and adapted to utilize other resources in addition to ungulate dung (Hallfter & Matthews 1966). Today, dung beetles can be found on all the continents except the Antarctica (Spector 2006).

The first Scarabaeinae beetles have been estimated to have dispersed to Madagascar about 64 to 44 million years ago based on timed phylogenies (Wirta et al. 2010). After that, ancestors of

the present dung beetles have spread to the island at least seven times. Four of the colonizations have led to extensive radiations that have generated the vast majority of the current endemic dung beetles in Madagascar – the subtribe Helictopleurina and the seven endemic genera in the tribe Canthonini: *Arachnodes, Apterepilissus, Epilissus, Apotolamprus, Cambefortatus, Nanos* and *Epactoides* (Wirta et al. 2008, Wirta et al. 2010, Miraldo et al. 2011). The other and probably more recent colonizations brought to Madagascar the tribes Onthophagini and Scarabaeini, which have currently only a few species that mostly inhabit open areas and dry forests. These colonizations did not lead to extensive radiations, probably because the dung beetle niches in forests were already occupied and open habitats offered relatively little resources (cattle was introduced to Madagascar only about 1500 years ago) (Wirta et al 2008).

Altogether, there are approximately 270 species of Scarabaeinae dung beetles in Madagacar, in addition to which there are around 30 species of Aphodiinae (Miraldo et al. 2011), which are not included in this study. The total number of Scarabaeinae in Madagascar is about twice the species number on other tropical islands of roughly same size such as Borneo and Sumatra. On the other hand, the species richness at the level of local communities (α-diversity) is relatively low in Madagascar (Viljanen et al. 2010a), most likely due to the limited range of resources in Madagascar, where there are no large-bodied native mammals (Miraldo et al. 2011). The high total species diversity in Madagascar has been suggested to be the result of long period of isolation and a wide range of habitats, which have facilitated speciation. Climatic changes during the Pleistocene and earlier may have caused changes in the distribution of vegetation and enabled allopatric speciation in forest refugia (Miraldo et al. 2011).

The relative scarcity and low diversity of resources in Madagascar has not only restricted the number of co-occurring dung beetle species locally but also influenced their evolution. On average, Malagasy dung beetles are smaller and there are more diet generalists than elsewhere in the tropics (Viljanen et al. 2010a). The two oldest radiations in Madagascar, Helictopleurina and the *Arachnodes* lineage, including the genera *Arachnodes, Apterepilissus* and *Epilissus,* include more dung specialists and vary more in body-size than the subsequent radiations, which is probably the result of the resources produced by lemurs and empty niches available at the time of their arrival (Wirta et al. 2008, Wirta et al. 2010, Miraldo et al. 2011). The subsequent colonizations and radiations, the *Epactoides* and *Nanos* lineages (the latter including *Apotolamprus*), have evolved in the presence of the earlier radiations and hence in a more

competitive environment. *Epactoides* are mostly small-bodied, relatively uncommon and occur in marginal conditions (Miraldo et al. 2011). *Nanos*, on the other hand, is a very abundant and successful group, which can be attributed to their more extensive use of carrion and opportunistic breeding behavior (Viljanen 2009).

Despite the fact that many Malagasy dung beetles are generalists in their resource use, no species use the introduced resource of cattle dung in forests. In contrast, a few species have been able to shift to use cattle dung as their primary resource in open areas (Hanski et al. 2007). Those species that have done so, including 4 species of Helictopleurina and a few *Arachnodes*, have probably originally inhabited dry forests and semi-open habitats, which has made it easier to switch to live in open habitats (Rahagalala et al. 2009). Open habitats are very different compared to forests in terms of their microclimatic conditions, and typical forest-dwelling dung beetles are adapted to the narrow thermal fluctuations of tropical forests (Sheldon et al. 2011). It is hence not surprising that the extensive deforestation has already caused the apparent extinction (actual extinction or extreme rarity) of some tens of forest-dwelling dung beetle species in Madagascar (Hanski et al. 2007).

1.4. Aims of this study

There is a need for further studies of the responses of insects and other invertebrates to forest degradation. Dung beetles have turned out to be a good model system for this purpose, but so far studies on dung beetles have been conducted in only a few tropical regions. Madagascar is a biodiversity hot-spot under serious threat of forest loss, and hence studies on the consequences of deforestation, forest fragmentation and the ability of degraded forest landscapes to support populations of the forest-inhabiting species are needed. Furthermore, such studies make a contribution to better understanding of dung beetle ecology in Madagascar, as previous studies have been mostly conducted in areas of primary or high-quality secondary forests in national parks.

In this thesis, I have studied dung beetle community structure within the highly fragmented area between Ranomafana National Park and the Vatovavy mountain in eastern Madagascar. I examine species diversity and species composition in forest fragments of different quality and degree of isolation from larger areas of primary forest. I pay particular attention to which kind of species persist in the fragmented forest landscape.

2 Previous research on dung beetles in altered tropical forest landscapes

Until 2007, studies of dung beetle responses to loss and fragmentation of rainforest were mainly focused on changes in the amount and spatial configuration of habitat and their impacts on species diversity. Following a review article in The Scarabaeinae Research Network (Nichols et al. 2007), more studies have examined the effects of qualitative changes in vegetation, temporal and spatial variation of habitat type, and dung beetle community structure in human-modified landscapes (Quintero & Halffter 2009). Furthermore, more research has been conducted on functional diversity of dung beetles and the effects of diversity losses on ecosystem functions such as nutrient cycling and seed dispersal (Slade et al. 2007, Slade et al. 2010, Barragán et al. 2011). The vast majority of the research has been conducted in Central and South America (Costa Rica, Guatemala, Mexico, Brasilia, Bolivia, Columbia, Peru, French Guiana and Venezuela), but there are also some studies from Africa (Ghana and Uganda) and Asia (Borneo and Indonesia) (Nichols et al. 2007).

2.1 Effects of fragment size

Habitat area is the most obvious factor that influences species diversity of forest-inhabiting dung beetles. Nearly all studies have detected a significant correlation between the size of rainforest fragment and local species richness. In continuous primary rainforest, there are always more species than in fragments, and smaller fragments sustain fewer species than larger ones. Also, in smaller fragments species composition is different from that in continuous primary forest (Nichols et al. 2007). Some studies have found that smaller fragments are dominated by a few very abundant species (Nichols et al. 2007, Diaz et al. 2010), in other words, the species abundance is less even in small fragments.

In addition to being few in number, the species in small fragments tend to be smaller in size than species in larger fragments and in continuous forest. Finally, the composition of species assemblages vary greatly between fragments (Quintero & Halffter 2009). Especially large tunnelers (dung beetles that process their food resource by burying it in tunnels below the dung pile or other resource) have been recorded to suffer from forest loss (Nichols et al. 2007, Quintero & Halffter 2009, Slade et al. 2007). This has been assumed to result from qualitative changes in vegetation and stronger edge effects, which benefits small-sized rollers (beetles that roll their food away before burial) that are more competitive in open habitats (Quintero &

Halffter 2009, Slade et al. 2007). Lack of large mammals in small fragments is also a probable cause for the loss of large dung beetle species (Feer & Hingrat 2005). Great variation in the species composition among fragments may result from the greater role of stochasticity in the assembly of communities in small areas (Feer & Hingrat 2005), but it can also reflect spatial heterogeneity in vegetation and other habitat properties (Quintero & Halffter 2009). Thus, it is important to consider the ecological differences between species before drawing conclusions about the effects of rainforest loss on dung beetle communities.

2.2 Connectivity

According to the metapopulation theory, viability of a metapopulation at the landscape level depends on the balance between local extinctions and establishments of new local populations (Hanski 1999). Thus, survival of species in human modified areas depend on their dispersal capacity, which is affected by species specific characteristics, distances between suitable habitat fragments and the composition of the habitat matrix (Saunders et al. 1991). Connectivity is a measure that describes the flow of dispersers between habitat patches in a landscape. Connectivity of a particular habitat patch can be measured as the distance to the nearest neighboring patch, but it is more realistic to consider the distances to and the sizes of all surrounding habitat patches. Such a measure of connectivity is the formula used in the Incidence Function Model (IFM) (Hanski 2005; see Section 3.3).

Research on the effects of fragment isolation (inverse of connectivity) on dung beetle communities has produced controversial results: in some studies increased isolation has resulted in reduced diversity whereas in other studies no effect was detected. The conflicting results may be due to qualitative differences between study areas and to confounding effects of matrix properties (Nichols et al. 2007). Also, in most studies isolation has been measured as the distance to continuous forest, which is a poor measure of connectivity in fragmented landscapes (Hanski 2005).

Dispersal of dung beetles and other animals can be facilitated by habitat corridors. Corridors offer dispersal routes but also add to the habitat area (Saunders et al. 1991). It has been found that at least some organisms can take advantage of corridors, but more information is needed about what kind of corridors function for different species. As forest dwelling-dung beetles are sensitive to microclimatic changes, it is not surprising that narrow “living fences” (hedgerows)

did not assist dispersal of dung beetles in a study by Diaz and others (2010). On the other hand, if a corridor is wide enough, it offers more living space and potential dispersal routes for both dung beetles and mammals that provide resources for them.

2.3 Changes in forest quality

Forest fragment size and connectivity are unlikely to explain all changes in community structure of dung beetles in human modified landscapes. Many contradictory results can potentially be explained by species-specific habitat requirements, variation in vegetation quality, habitat matrix structure and temporal variation. Since the review by Nichols and her research group (2007), these factors have been increasingly studied.

Vegetation quality and microclimate are thought to be the most significant factors affecting dung beetle species assemblages. For example, in a study by Navarrete and Halffter (2008), canopy coverage and land surface temperature had the strongest effects on dung beetle community structure. It is obvious that these features are very different in primary forests and in clear cuts, but vegetation and microclimate vary continuously between these extremes. In contrast to herbivorous beetles like Chrysomelidae, vegetation age or species composition does not matter for dung beetles (Quintero & Halffter 2009). For example, it has been observed that coffee and cocoa plantations can support part of the original rainforest dung beetle assemblage (Nichols et al. 2007).

The transition zone in vegetation structure at forest edges can be sharp or gradual. In fact, habitat matrices between fragments are rarely homogenous but rather mixtures of agricultural land and secondary vegetation of different successional stages. In such cases, it may be very difficult to tell where the forest ends and the matrix begins. Secondary vegetation and plantations around fragments can significantly reduce edge effects and facilitate dispersal between forest fragments (Nichols et al. 2007). One of the first studies about the effects of matrix structure and temporal variation in vegetation (Quintero & Roslin 2005) revealed a sharp contrast between forest fragments and their surroundings exacerbated dispersal of dung beetles. However, 15-year-old secondary vegetation around the fragments supported nearly all of the species in fragments. In addition, development of secondary vegetation allowed the colonization of fragments by some large species of dung beetles that had been lost by

fragmentation, and the distribution of species abundances became more similar in fragments and continuous forest.

In addition to providing suitable microclimate for dung beetles, vegetation has also to satisfy the habitat requirements of the mammals that provide the resources for dung beetles. A likely reason why large dung beetle species disappear first from small fragments is the disappearance of large mammals from small fragments. The linkage between mammal abundance and dung beetle diversity has been studied especially with howler monkeys in Central America, where dung beetle abundances have become greatly reduced following the disappearance of the primates from small and isolated forest fragments (Estrada et al. 1999). Quintero and Halffter (2009) also noticed the importance of mammals in their study about temporal changes in vegetation. As vegetation regrowth brought back some of the food plants of howler monkeys and sloths, dung beetle species specializing on the dung of these animals returned following the return of the mammals.

One should take into account the influence of temporal changes in vegetation structure while evaluating the effects of rainforest loss and fragmentation on dung beetles. According to Quintero and Roslin (2008) and Quintero and Halffter (2009), regrowth of secondary forest improves the viability of many dung beetle species already at the age of 15 years. On the other hand, lack of knowledge about temporal variation may give a too optimistic picture about species survival. This is because immediately following forest destruction species diversity may even increase in the remaining forest fragments due to a phenomenon called “super saturation”, in which populations are packed into the remaining suitable habitat patches (Saunders et al. 1991). Following the short initial period, the less competitive species start disappearing until community structure is stabilized at the level the remaining habitat can support. The term "extinction debt" refers to the number of species that will eventually go extinct because of past environmental change but may persist in a transient state for a shorter or longer period of time (Hanski 2005). Therefore, following recent forest loss, species diversity will probably decline for some time.

2.4 Functional consequences of dung beetle species loss

Dung beetles contribute to important ecosystem functions, such as nutrient cycling, bioturbation (aeration of soil) and secondary seed dispersal. In addition, dung beetles have been recognized to reduce the numbers of flies and many parasites by competing for the same resource. A few species of dung beetles also serve as pollinators. The significance of dung beetles in ecosystems has been studied especially in savannas and grasslands, but dung beetles can be assumed to play a substantial role also in rainforests, where competition is intense (Nichols et al. 2008). Recent studies have supported this conjecture (e.g. Slade et al. 2007, Slade et al. 2010, Barragán et al. 2011).

According to Slade (2010), removal of dung and seeds by dung beetles is significantly reduced in intensely modified rainforests. The efficiency of dung and seed removal is related to dung beetle species richness, and especially the absence of large tunnelers weakens these functions (Slade et al. 2007, Barragán et al. 2011). No reduction in efficiency due to competition between the species were observed, on the contrary, different functional groups of dung beetles seem to complement each other (Slade et al. 2007). These results support the previous hypotheses about the crucial role of large-sized species of dung beetles in ecosystem functioning (Nichols et al. 2007). Therefore, especially the extinctions of the most effective species, large nocturnal tunnelers, may in the long run cause problems in nutrient cycling and benefit wind dispersing plants over those dispersing with the help of animal vectors (Slade et al. 2010). Similar views have been presented by several researchers. For example Didham and his colleagues (1996) have estimated that the loss of dung beetles may have serious impacts on rainforest primary production and regeneration.

3 Material and methods

3.1 Study areas and sampling

The field work for this study was conducted in southeastern Madagascar between two areas of primary humid forest: the Ranomafana National Park and the Vatovavy mountain (Fig. 1). Between these areas, the landscape consists mostly of agricultural land (mainly rice fields, cassava and fruits), forest fragments of different size and quality as well as secondary vegetation.

The average rate of forest loss in the unprotected part of the study area has been estimated to be 1.2%/yr between 1990-2000 and 1.5%/yr 2000-2005 (Puhakka 2012).

Sampling of dung beetles was conducted in 44 locations within areas of degraded vegetation and 11 locations in primary forest (Fig. 1, Appendix 1). The sampling period lasted two months from mid-November in 2011 until mid-January in 2012. This time period was chosen for sampling because the abundance of Malagasy dung beetles has been recorded to be highest in the early rainy season (December-February) (Viljanen et al. 2010b).

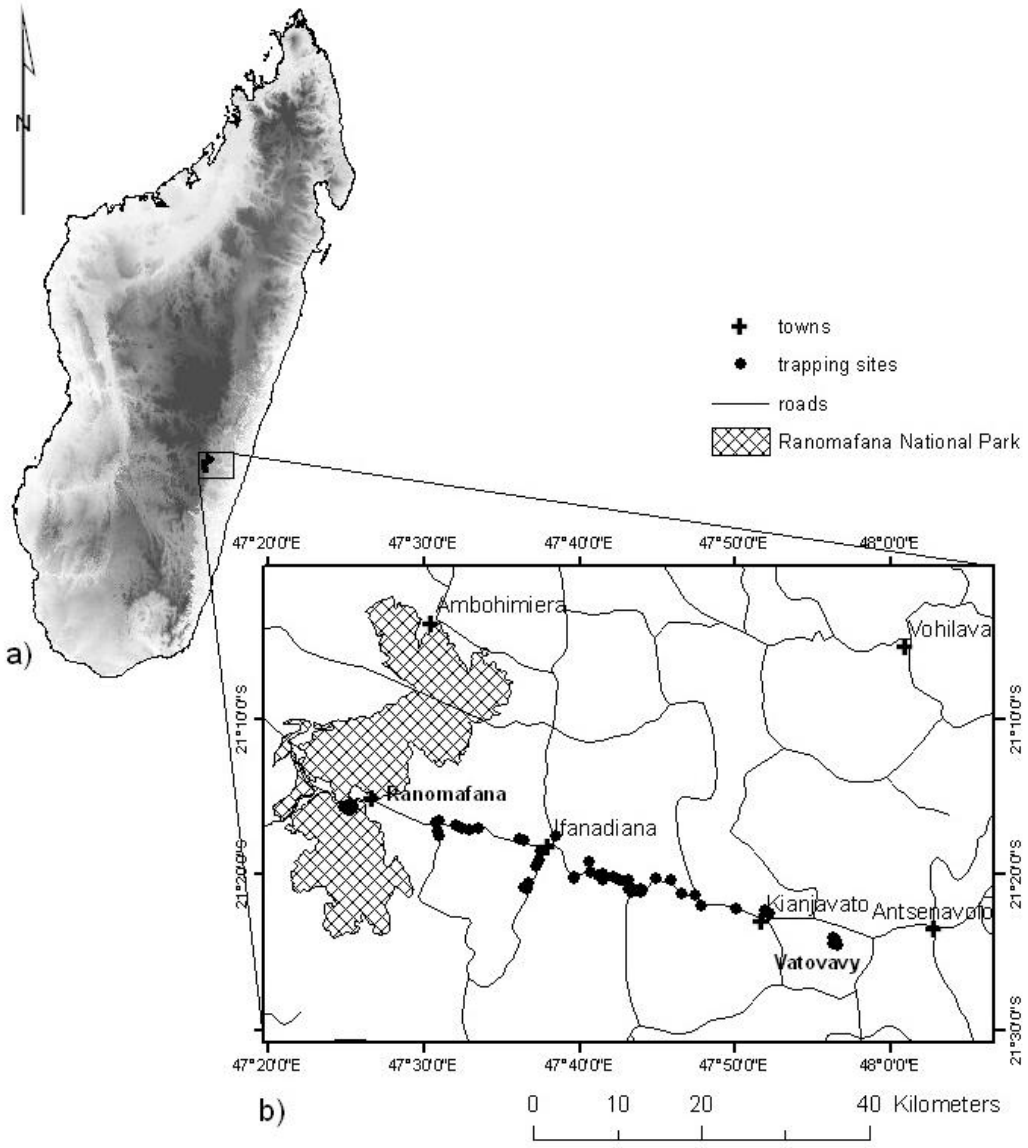

Figure 1. The locations of a) Ranomafana National Park (RNP) in eastern Madagascar and b) the study sites between RNP and the Vatovavy mountain.

The Ranomafana National Park (RNP) is part of one of the largest remaining areas of primary rainforest in Madagascar. It is located in southeastern Madagascar (47°18'–47°37' E, 21°02'–21°25' S) and covers 43,500 ha of mid-elevation rainforest at elevations ranging from 400 to 1,400 m asl. Trappings in RNP were conducted in the Talatakely area (900 m asl), close to the entrance of the national park. The Vatovavy mountain (47°56' E, 21°24' S) lies about 50 km south-east from Ranomafana (Fig. 1) and comprises 1,600 ha of unprotected lowland rainforest at elevations from about 150 to 500 m asl, which has remained relatively undisturbed owing to its sacred status in local culture.

Sampling was conducted by setting up transects of 30–60 pitfall traps, one per each locality in the degraded forest area, and six and five in Ranomafana and Vatovavy, respectively. The traps were plastic cups (0.5 dl) covered by a big leaf to prevent the cup from filling up with rain water. About a fifth of the volume was filled with water with a drop of detergent to reduce surface tension. The traps were baited with a piece of approximately 4 cm^3 of either fish (*Tilapia*) (Fig. 2) or chicken intestine, which have been observed to attract at least 80% of forest dwelling Malagasy dung beetles (Viljanen et al. 2010b). The duration of trapping was two days at most localities, with a few exceptions of one or three days.

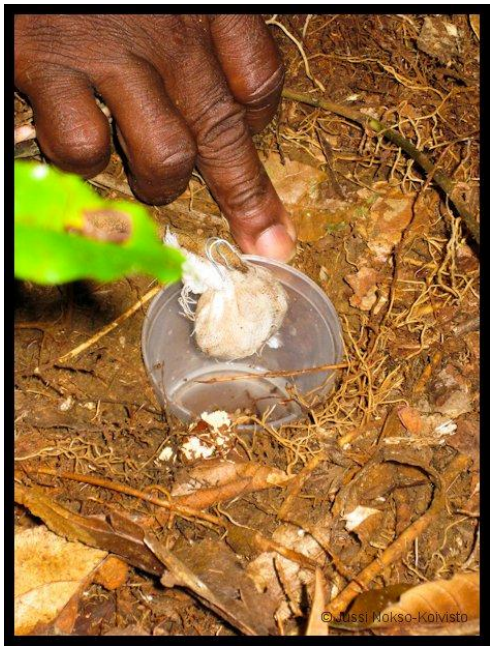

Figure 2. Fish-baited pitfall trap.

Figure 3. EL-USB-2 datalogger set up 20 cm above groud.

In each locality, several variables describing vegetation structure and quality were measured. The quality of the vegetation was rated according to the degree of human impact using six classes, which are described in Table 1.

Table 1. Description of vegetation classes.

Class	Description
1	shrubbery with no large trees
2	shrubbery with a few larger trees
3	open degraded forest with much human impact (e.g. trails, tree plantations, cut trees)
4	closed degraded forest with some human impact (e.g. largest trees removed)
5	closed degraded forest with little human impact (e.g. trails)
6	primary forest

The hights of the clearly visible vegetation layers were measured with a hypsometer and tree density was estimated with relascope. The direction and steepness of the slope, on which the trapping transect was set up, was estimated. Temperature (20 cm above ground) and humidity were measured with EL-USB-2 dataloggers (Fig. 3) with 1 hour observation interval during the trapping period.

Samples were preserved in ethanol. Following the field work, all specimens were transported to University of Helsinki, Finland, for identification. All dung beetle species excluding Aphodiinae were identified, except a few individuals that were possible to identify to the genus level only. These beetles were sent to Dr. Olivier Montreuil in the Paris Museum of Natural History for further study, which is still in process. In this thesis, these individuals are referred to with code names and the names based on the preliminary identification denoted with abbreviation cf.

3.2 Spatial analyses

To describe the spatial structure of the vegetation around the sampling sites, I calculated connectivity values for each transect. This was done with ArcGIS (version 9.0) and the satellite image –based land cover classification of the Ranomafana area that has been produced by Puhakka (2012). In this classification, the landscape was divided into seven categories: primary forest, secondary forest, degraded forest/dense bushes, shrubbery (open, < 3 m vegetation), human affected non-forest, water, and open habitat.

Connectivity (S) was calculated by applying the formula (Hanski 1999):

$$S_i = \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j$$

This formula is usually used for landscapes consisting of discrete habitat patches. In such cases, *i* is the patch for which the connectivity is measured, *j* is another patch, and d_{ij} is the distance between the two patches. The dispersal capacity of the species is described by the constant α; the inverse 1/α gives the average dispersal distance (Hanski 1999). The contribution of patch *j* to the connectivity of patch *i* is furthermore weighted by the area of patch *j*, A_j. Connectivity thus defined measures structural connectivity of the landscape, as there is no information about the occurrence of the focal species in the landscape. In the present study, the borders of the patches were impossible to determine accurately because of much variation in vegetation quality between the trapping sites and lack of clear edges around the trapping sites. Therefore, instead of measuring the connectivity of one patch to the surrounding habitat patches, I measured connectivity of the mid-point of a transect (*i*) to the amount of forest at different distances from it.

Four different connectivity values were calculated for each location using the first four vegetation categories in Puhakka's (2012) classification. The first connectivity measure was calculated by taking into account only the primary forest, the second measure by taking into account primary and secondary forests, the third one by including primary, secondary and degraded forests, and the fourth one by including all vegetated categories (forests and shrubbery). To calculate S_i, I first calculated with ArcGIS the areas (m²) of vegetation in the four categories at different distances from the trapping site (*i*). This calculation was done by defining buffers around the trapping site at 100 m intervals until 1,000 m, and by summing up the areas (m²) of forest in each category within each buffer. In this case, d_{ij} is the distance between *i* and the mid-point of the buffer. I repeated the calculations for 3 values of α, namely 1/30, 1/100 and 1/500, which correspond to average dispersal distances (1/α) of 30 m, 100 m and 500 m. These values are considered to be realistic dispersal distances for dung beetles (Viljanen 2009, I. Hanski pers. comm.).

3.3 Statistical analyses

SPSS (PASW statisticts 18) was used for most statistical analyses and to prepare figures. In addition, some figures like the temperature chart and the rarefaction curves were drawn in Microsoft Office Excel. The rarefaction curves were calculated with web-based calculator provided by John Brzustowsky (http://www2.biology.ualberta.ca/jbrzusto/rarefact.php) and they were used to estimate the adequacy of the sample size (Gotelli & Colwell 2001). Correlations between species diversity and landscape variables were analyzed with general linear models (Grafen & Hails 2002). *P* values less than 0.05 were considered to be significant.

Patterns in species distributions and landscape variables were further examined with principal components analysis (McGarical et al. 2000). Only the most common species were included in the analysis, using the following criteria: Kaiser-Meyer-Olkin Measure of Sampling Adequacy > 0.6, and Bartlett's Test of Sphericity significant. While analyzing the landscape variables, only connectivity (*S*) values calculated with $\alpha = 1/30$ were used to reduce the numbers of correlated variables.

4 Results

4.1 Temperature and humidity at the sampling sites

The weather of the study period was typical for the season. In November, rainfall was low and maximum daily temperatures varied between 24 and 33.5°C. Rains increased towards the rainy season, and maximum daily temperatures decreased to 22–27.5°C in January. The daily average humidity at the trapping sites varied between 82% and 100%. The maximum temperatures at the trapping sites were systematically 5–10 degrees higher than the reference temperatures in Talatakely, but they follow the same general pattern of temperature fluctuations (Fig. 4).

The minimum temperatures at the trapping sites do not follow the reference temperatures as well as the maximum temperatures. Significant correlations were found between minimum temperatures, altitude and vegetation quality (Table 2), but not between maximum temperatures, altitude and vegetation (Table 3). The relationships between the minimum temperature, altitude and vegetation class (Table 1) have been illustrated in Fig. 5.

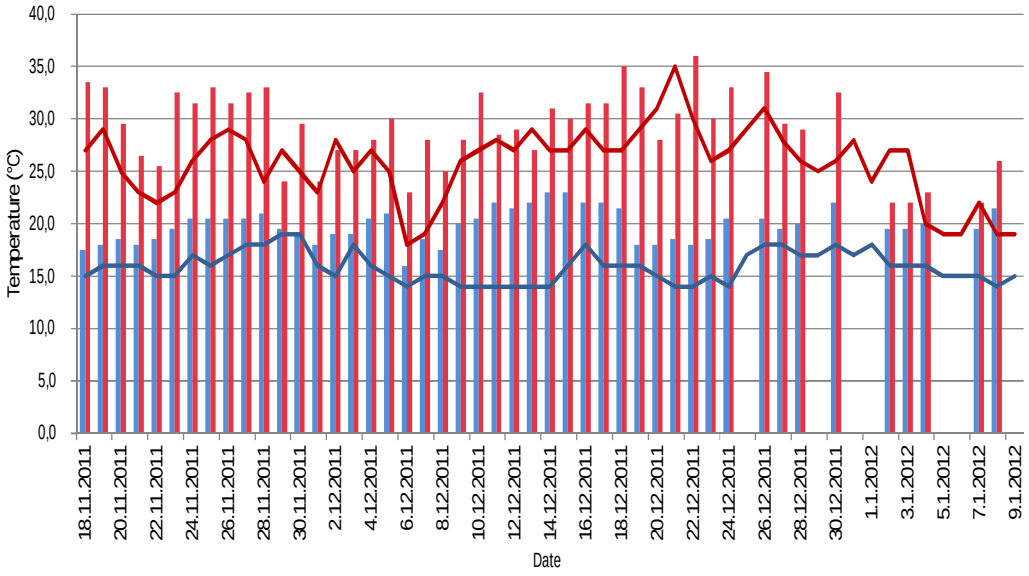

Figure 4. Columns represent the minimum (blue) and maximum (red) temperatures during the trapping period at each transect. Lines show the reference temperatures measured at Talatakely by Centre ValBio.

Table 2. Analysis of variance of the effects of reference temperature, vegetation class and altitude on minimum temperature at the trapping sites.

Source	Type III Sum of Squares	df	Mean Square	F	P
Intercept	85.2	1	85.2	113.8	< 0.001
Minimum temp. (ref)	4.0	1	4.0	5.4	0.027
Altitude	43.4	1	43.4	58.0	< 0.000
Vegetation class	22.4	5	4.5	6.0	< 0.000
Error	25.5	34	0.8		
Total	16895.0	42			
Corrected Total	95.0	41			

Adjusted $R^2 = 0.68$

Table 3. Analysis of variance of the effects of reference temperature, vegetation class and altitude on maximum temperature at the trapping sites.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	114.0	1	114.0	16.6	< 0.001
Maximum temp. (ref)	247.6	1	247.6	36.0	< 0.001
Altitude	0.1	1	0.1	0.01	0.919
Vegetation class	44.3	5	8.9	1.3	0.291
Error	233.6	34	6.9		
Total	37259.5	42			
Corrected Total	531.8	41			

Adjusted $R^2 = 0.47$

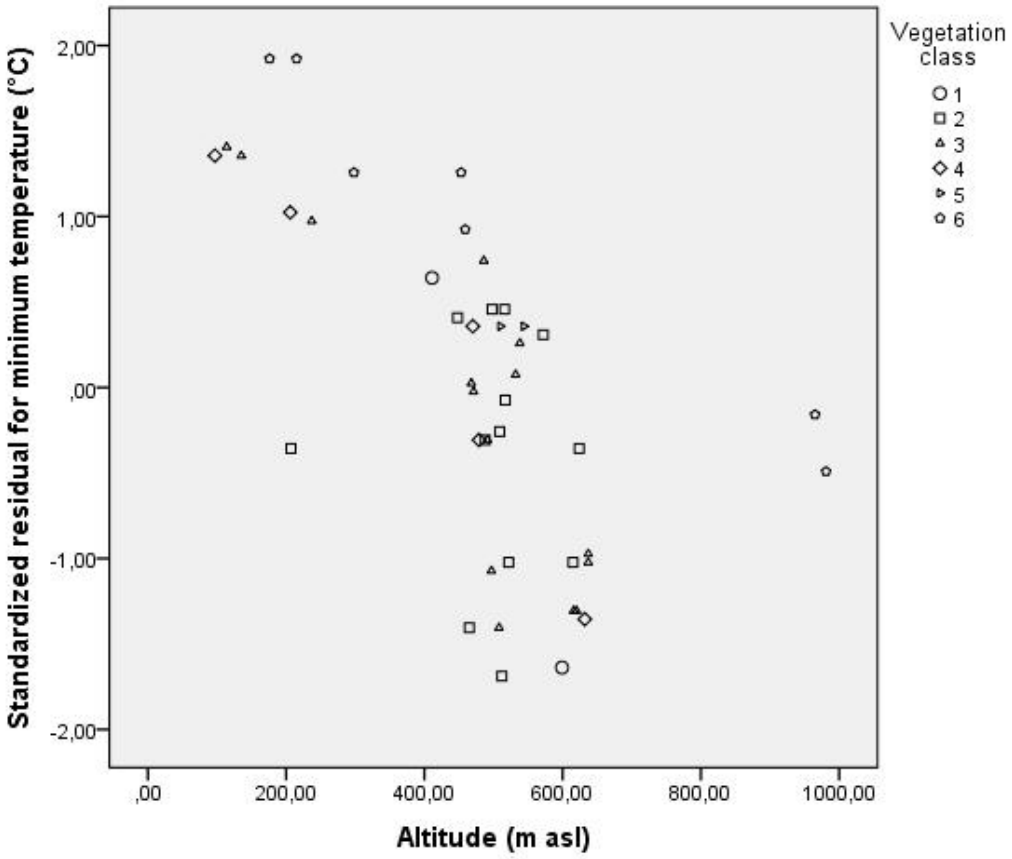

Figure 5. Relationships between minimum temperature (C°), altitude (m asl) and vegetation class (1–6, [Table 1]).

4.2 Division of transects into seven zones

The study sites were divided into seven zones in terms of forest area, distance from the Ranomafana National Park, average connectivity of transects, and elevation. The division of transects into the zones is illustrated in Fig. 6. The first zone (I) from the west, Talatakely, includes transects that were set inside the Ranomafana National Park. The average elevation of the transects in this zone was 960 m asl. Talatakely area is located near the entrance of the park. There was some selective logging in this area at the end of the 1980's. Even though the area has been regenerating since it became protected in 1991, there are still more signs of human impact, like secondary vegetation, trails and pioneer species, than in the rest of the park (Wright & Andriamihaja 2002).

The second zone (II) includes transects in the proximity of the villages of Morafeno and Kelilalina. This area is badly degraded and most transects were set up in open vegetation of

classes 1–3. Only one transect was set up in a forested fragment with relatively closed canopy (class 4). The average elevation of the transects was 623 m asl.

The surroundings of Ifanadiana and Tsaramasoandro comprise zone III and include many high-quality fragments. The vegetation in two fragments was classified as 5, while most of the other transects were of class 3. The average elevation of the transects was 482 m asl.

Zone IV has 18 transects around the villages of Antanambao and Ambodihazo at the average elevation of 511 m asl. Relatively large and high-quality fragments were found especially in the eastern part of this zone, but many of them were not accessible to us because they were consecrated by the locals for graves and spirits. The vegetation in those that we were allowed to enter was of classes 2–4. Zones III and IV are similar by their vegetation and elevation, but they are separated by a few kilometers with little forest remaining. Zone III is closer to Ranomafana, and zone IV is closer to lowland forests in the Kianjavato area and Vatovavy.

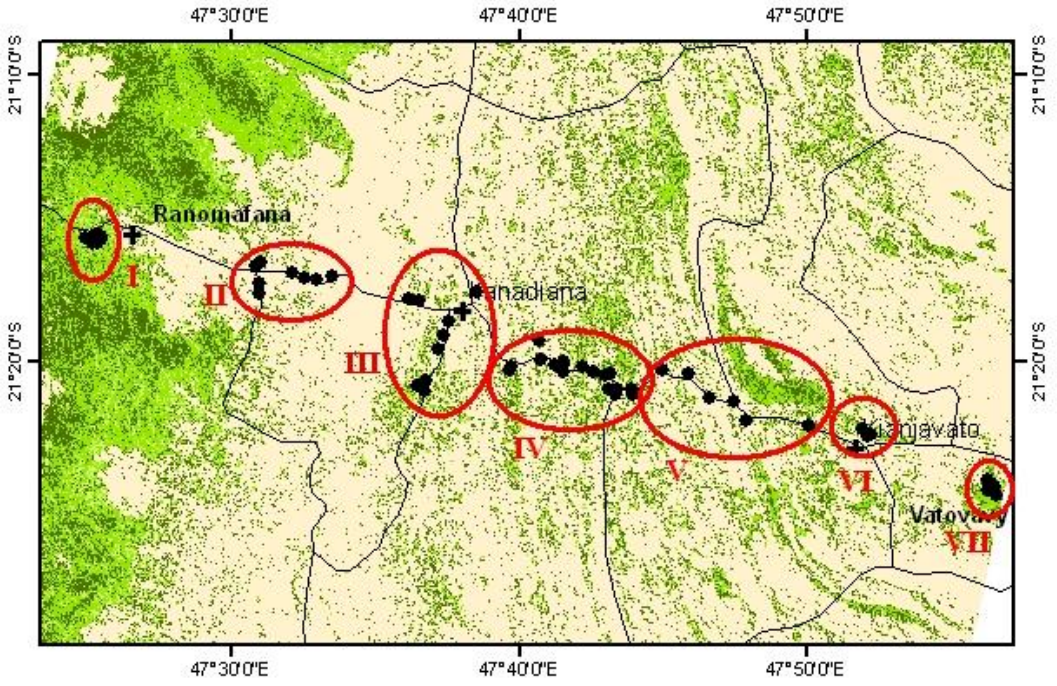

Figure 6. The division of transects into seven zones (I-VII) characterized by similar vegetation qualities. The numbering proceeds from the west (Ranomafana) to the east (Vatovavy).

On the eastern side of the four first zones the altitude decreases sharply by about 300 meters. Zone V is located on this transition area with steep eroded slopes and badly degraded vegetation. True forest was very difficult to find, and only two transects were set up in vegetation of class 3, the other 4 in fragments of class 2. The average elevation of these transects was 232 m asl.

Zone VI consists of three transects that were set up in Sangasanga forest, which is a coffee production and research area owned by FOFIFA (FOibe FIkarohana ampiharina amin'ny Fampandrosoana ny eny Ambanivohitra, the National Center for Rural Development) in Kianjavato village. Sangasanga comprises a mixture of open coffee fields, forest-covered coffee plantations, secondary rainforest and bamboo. It is also connected to a wider mountainous primary forest fragment of Tsitola on its southwestern side and is well-known for supporting a diverse community of lemurs, including greater bamboo lemur, red-fronted brown lemur, black-and-white ruffed lemur and aye-aye (McGuire et al. 2009). The transects in Sangasanga were set up in vegetation of classes 3 and 4 at elevation of 146 m asl on average.

The final zone VII comprises 5 transects in high quality primary forest on the slopes of the Vatovavy mountain. The average elevation of these transects was 320 m asl.

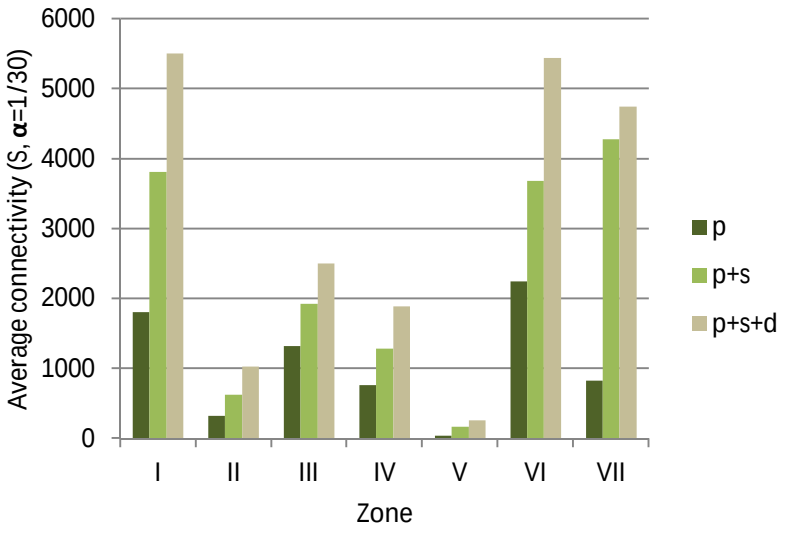

Figure 7. Average connectivities (for α=1/30) of transects within each zone. Connectivities have been calculated separately for primary forest (p), primary + secondary forest (p+s), and primary+secondary +degraded forest (p+s+d).

In addition to general vegetation quality, connectivity was dissimilar among the zones. The average connectivities ($\alpha = 1/30$) for transects within 1 km radius were calculated for each zone (Fig. 7). The values differ to some extent depending on whether they were calculated for primary forest only, primary and secondary forests or all forested vegetation types. The general pattern is that Talatatakely, Sangasanga and Vatovavy (zones I, VI and VII) are best connected followed by the Ifanadiana and Ambodihazo areas with lower total connectivities but relatively good state of primary forest connectivity. Zones II and V are clearly most isolated, transects in the latter showing little or no connectivity in relation to forested vegetation types.

4.3 Species composition and abundances in different zones

Altogether, 4,199 individuals representing 24 different species were sampled (Appendices 2 and 3). The vast majority, 19 species with 3,848 individuals, were Canthonini, while 5 species with 351 individuals were Helictopleurini. Thirty-two individuals representing 6 species (5 *Arachnodes* and 1 *Nanos*) could not be identified with the help of the University of Helsinki collections. They were sent to the Museum of National History in Paris for further study. It is possible that some of these individuals belong to formerly unknown species.

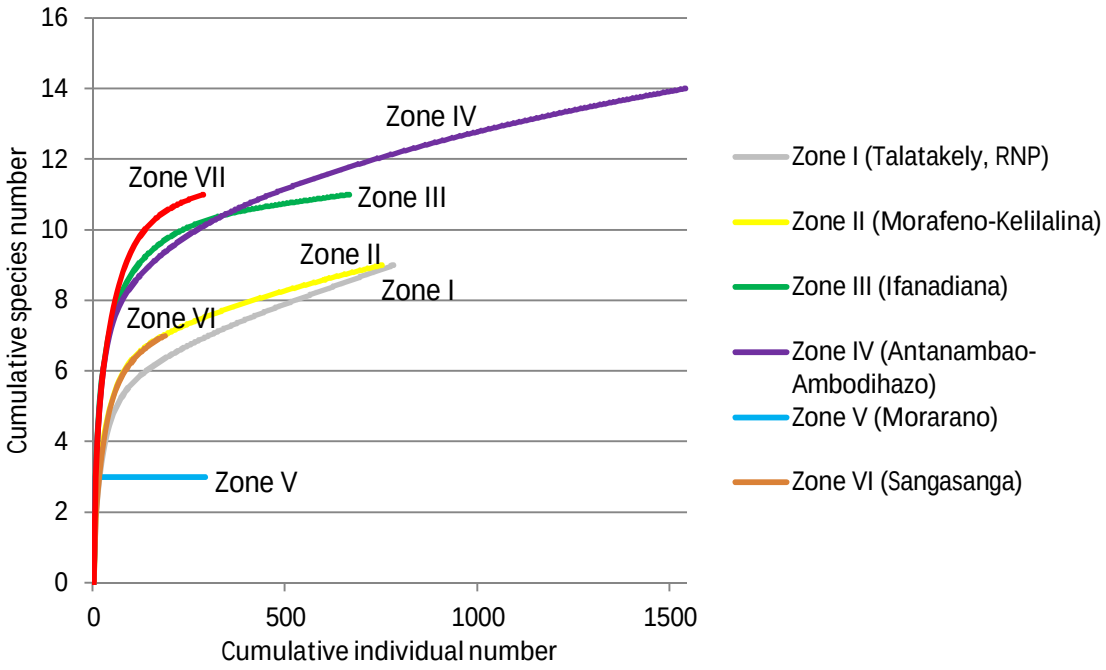

Figure 8. Species accumulation curves for each zone.

Figure 8 shows the rarefaction curves for the seven zones. None of the curves has clearly reached an asymptote, and therefore increasing the sample size would undoubtedly add new species. However, some trends in the results are noteworthy. Vatovavy, Antanambao-Ambodihazo and Ifanadiana clearly differ from the rest with much higher species numbers, Kelilalina-Morafeno, Sangasanga and Talatakely are in the middle group and Morarano only had three species. Three to fourteen species were found per zone. The most species rich was zone IV and the poorest zone V. Among single transects, the most species rich was transect 21 in zone IV, with 14 species. The vegetation around this transect was classified as only 2, but the transect was located in the heart of Ambodihazo and surrounded by several large and high quality fragments. The numbers of individuals per species in each zone are presented in Table 4, and the results for each transect are given in Appendix 1. Below, I describe the results for each zone in more detail.

In Talatakely (zone I), altogether 9 species were collected. Eight of them (*Apotolamprus helenae*, *A. quadrinotatus*, *Epactoides frontalis*, *Epilissus apotolamproides*, *E. delphinensis*, *Helictopleurus fasciolatus pseudofasciolatus*, *H. rudicollis* and *Nanos viettei*) are among the most common species previously sampled from the area (Table 5), whereas one *Nanos* (*Nanos* cf. group *minutus*) could not be identified to species level with the help of the University of Helsinki collections. Not surprisingly, my samples did not include the common dung specialist species previously sampled from Talatakely (Table 5), as I only used fish and chicken intestine bait in trapping.

In the area around Morafeno and Kelilalina (zone II), 9 species were sampled. Five of the species were common with Talatakely (*Apotolamprus helenae, Epilissus apotolamproides, E. delphinensis, Helictopleurus fasciolatus pseudofasciolatus and Nanos viettei*), and in addition there were four small-sized species (*Apotolamprus manomboensis*, *Aracnodes* cf. group *luctuosus*, *Epactoides major* and *Helictopleurus viridiflavus*) that were not present in the sample from Talatakely.

The sample collected from the fragments around the first larger town east of Ranomafana, Ifanadiana (zone III), included 11 species. Four common species that were present in Talatakely and Morafeno-Kelilalina, were found also here. In addition, *Apotolamprus quadrinotatus*, *Nanos*

cf. group *minutus*, *Arachnodes* cf. *pusillus*, *A.* ARARANO11A, *Epactoides major* (common with Morafeno-Kelilalina) and *Helictopleurus viridans* were collected in zone III.

The area between Antanambao and Ambodihazo (zone IV) turned out to be the most diverse one with 14 species sampled. Half of them (7 species) were common with Talatakely (the five most common ones plus *Apotolamprus quadrinotatus* and *Nanos* cf. group *minutus*) and five of them were common with zones II and III (*Arachnodes* ARARANO11A, *A*. cf. *pusillus*, *Epactoides major*, *Helictopleurus viridans* and *H. viridiflavus*). Additionally, there were two more unidentified *Arachnodes* species (*A*. ARARANO11B and *A*. cf. group *angulosus*).

Table 4. Species composition and abundances in each zone.

	Zone I Talatakely	Zone II Morafeno-Kelilalina	Zone III Ifanadiana	Zone IV Antanambao-Ambodihazo	Zone V Morarano	Zone VI Sangasanga	Zone VII Vatovavy
Apotolamprus helenae (Montreuil, 2004)	4	115	131	399	1	1	
Apotolamprus manomboensis (Montreuil, 2006)		1					
Apotolamprus quadrinotatus (Boucomont, 1937)	1		5	67			
Arachnodes ARARANO11A			7	9			
Arachnodes ARARANO11B				3			
Arachnodes cf. group *angulosus*				1			
Arachnode s cf. group *luctuosus*		1					
Arachnodes cf. *pusillus*			1	2			
Epactoides frontalis (Montreuil, 2003)	1						
Epactoides mahaboi (Paulian, 1976)						2	
Epactoides major (Paulian, 1991)		20	54	95			5
Epactoides tiinae (Montreuil, 2005)							1
Epilissus apotolamproides (Lebis, 1961)	16	18	27	47		8	6
Epilissus delphinensis (Lebis, 1953)	64	14	23	116			16
Epilissus emmae obscurpennis (Montreuil, 2006)						11	5
Epilissus prasinus (Klug, 1832)						7	69
Helictopleurus fasciolatus pseudofasciolatus (Montreuil, 2007)	30	32	72	78	3	4	4
Helictopleurus quadripunctatus (Olivier, 1789)					1		
Helictopleurus rudicollis (Fairmaire, 1898)	27						
Helictopleurus viridans (Fairmaire, 1901)			18	12			9
Helictopleurus viridiflavus (Fairmaire, 1898)		3		1			
Nanos bimaculatus (Künckel, 1887)						150	130
Nanos cf. group *minutus*	1		4	1			2
Nanos viettei (Paulian, 1976)	634	549	320	706			34

The surroundings of Morarano (zone V) was the most species poor area, with only four individuals belonging to two forest-dwelling species that were common in Talatakely and zones II and III (*Apotolamprus helenae* and *Helictopleurus fasciolatus pseudofasciolatus*). In addition, one individual of *Helictopleurus quadripunctatus*, species specialized on cattle dung in open areas (Rahagalala et al. 2009), was collected.

Table 5. Species composition of dung beetles (Scarabaeinae) and the total number of individuals sampled in Ranomafana National Park. My results are compared with the results of intensive trapping by H. Viljanen in 2003-2006. The species classification has been updated. The column "Diet" indicates the diet of each species (Viljanen et al. 2010). DS = dung specialist, G = generalist, C = carrion specialist, C* = traps baited with carrion at the trapping site, D† = tree traps baited with dung. The figures in the parentheses give the numbers of individual captured by Viljanen in the Talatakely area.

	Diet	Viljanen 2003-2006: Total number of individuals	Torppa 2011: Total number of individuals
Helictopleurini			
Helictopleurus carbonarius (Lebis 1960)	C*	1	
H. corruscus (d'Orbigny 1915)	DS	27 (24)	
H. dorbignyi (Montreuil 2005)	DS	13 (13)	
H. fasciolatus (Fairmaire1898)	G	118 (17)	30
H. giganteus (Harold 1869)	DS	2 (2)	
H. heidie (Montreuil 2007)	C*	1 (1)	
H. rudicollis (Fairmaire 1898)	G	299 (265)	27
H. semivirens (d'Orbigny 1915)	DS	174 (173)	
H. steineri (Paulian and Cambefort 1991)	G	46 (23)	
H. viridiflavus (Fairmaire 1898)	DS	4 (4)	
Canthonini			
Epactoides frontalis (Montreuil 2003)	G	44 (18)	1
E. helenae (Montreuil 2005)	C*	10	
E. incertus (Lebis 1953)	C*	7 (3)	
E. major (Paulian 1991)	G	54 (12)	
E. vaguecarinatus (Lebis 1953)	C*	1	
Apotolamprus helenae (Montreuil 2004)	C*	133	4
A. manomboensis (Montreuil 2008)	C*	10(5)	
A. perinetensis (Montreuil 2008)	C*	4	
A. quadrinotatus (Boucomont 1937)	G	342 (198)	1
Arachnodes hanskii (Montreuil 2003)	DS	331 (294)	
A. pusillus (Lebis 1953)	G	11	
A. robinsoni (Boucomont 1937)	D†	7 (7)	
A. seminitidus (Lebis 1953)	D†	10 (10)	
Cambefortatus ranomafanaensis (Montreuil 2008)	C*	15	
Epilissus antoetrae (Paulian 1975)	C*	3	
E. apotolamproides (Lebis 1961)	G	204 (164)	16
E. delphinensis (Lebis 1953)	C	451 (173)	64
E. emmae obscuripennis (Montreuil 2006)	C*	6	
E. genieri (Montreuil 2006)	DS	46 (34)	
E. mantasoae (Paulian 1976)	G	279 (86)	
Nanos bimaculatus (Künckel 1887)	C*	99	
N. rubromaculatus (Künckel 1887)	C	7 (7)	
N. viettei (Paulian 1976)	G	6309 (4301)	634
Nanos cf. group *minutus*			1

The species assemblage in Sangasanga (zone VI) differed much from the previous zones. Altogether 7 species were collected, of which only 3 were common with Talatakely and zones II to IV (*Apotolamprus helenae*, *Epilissus apotolamproides* and *Helictopleurus fasciolatus pseudofasciolatus*). In addition to these species, *Epactoides mahaboi*, *Epilissus emmae obscurpennis*, *Epilissus prasinus* and *Nanos bimaculatus* were collected.

At the Vatovavy mountain (zone VII), 11 species were collected. The sampling was conducted at three different elevations which differed in their species composition. Five species were collected at all elevations (*Epilissus emmae obscurpennis*, *E. prasinus*, *Helictopleurus fasciolatus pseudofasciolatus*, *Nanos bimaculatus*), one at only low elevations (170–215 m asl) (*Epactoides tiinae*), one at low and mid-elevations (170–300 m asl) (*Helictopleurus viridans*), three at mid- and high elevations (300–460 m asl) (*Epactoides major*, *Epilissus apotolamproides* and *E. delphinensis*) and two at only high elevations (350–360 m asl) (*Nanos viettei* and *Nanos* cf. group *minutus*).

4.4 Body sizes of beetles in different trapping zones

I divided the species into body length categories (Table 6) and analyzed differences in the numbers of beetles in the different trapping zones. The numbers of small and medium-sized (< 8 mm) species (Table 7) and large and very large (> 8 mm) species (Table 8) varied significantly between the different zones. Small and medium-sized species dominated in zones I to IV, and large and very large species dominated in zones V to VII (Fig. 9). Recall that in zone V only a few individuals were collected (Table 4) and zones VI and VII are the good quality secondary forests (classes 3 to 4) in Sangasanga and the primary forests (class 6) in Vatovavy (Section 4.2).

Next, I tested whether the proportions of small and medium-sized (< 8 mm) species in the different trapping transects depended on connectivity (S_1), altitude and vegetation quality. The results show that the proportion of small and medium-sized species was greater at higher elevations and in transects with more degraded vegetation classes (Table 9, Fig. 10).

Table 6. Classification of species into body length categories.

Species	Size	Source	Category
Nanos cf. group *minutus*			
Epactoides tiinae	3 mm	Montreuil 2005	SMALL < 5 mm
Epactoides mahaboi	3,25 mm	Paulian 1976	
Apotolamprus quadrinotatus	4 mm	Viljanen et al. 2010a	
Epactoides frontalis	4-5 mm	Viljanen et al. 2010a	
Epactoides major	3,5-4 mm	Viljanen et al. 2010a	
Arachnodes ARARANO11A			MIDDLE-SIZED 5-8 mm
Arachnodes ARARANO11B			
Arachnodes cf. group *angulosus*			
Arachnodes cf. group *luctuosus*			
Arachnodes cf. *pusillus*			
Apotolamprus helenae	5,5-7,5 mm	Viljanen et al. 2010a	
Apotolamprus manomboensis	6-7 mm	Viljanen et al. 2010a	
Helictopleurus viridiflavus	5-7 mm	Viljanen et al. 2010a	
Nanos viettei	6,5-7 mm	Viljanen et al. 2010a	
Nanos bimaculatus	8 mm	Viljanen et al. 2010a	LARGE 8-10mm
Epilissus apotolamproides	9-10 mm	Viljanen et al. 2010a	
Helictopleurus pseudofasciolatus	8-13 mm	Viljanen et al. 2010a	
Helictopleurus rudicollis	9-12 mm	Viljanen et al. 2010a	
Helictopleurus viridans	9,5-10 mm	Viljanen et al. 2010a	
Helictopleurus quadripunctatus			VERY LARGE > 1 cm
Epilissus delphinensis	10-14,5 mm	Viljanen et al. 2010a	
Epilissus emmae obscurpennis	10-14,5 mm	Viljanen et al. 2010a	
Epilissus prasinus			

Table 7. One-way ANOVA on the number of small and medium-sized (< 8 mm) species in different trapping zones.

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	36.5	6	6.1	3.4	0.008
Within Groups	69.1	39	1.8		
Total	105.5	45			

Table 8. One-way ANOVA on the number of large and very large (> 8 mm) species in different trapping zones.

	Sum of Squares	df	Mean Square	F	Sig.
Between Groups	23.9	6	4.0	3.4	0.008
Within Groups	47.6	41	1.2		
Total	71.5	47			

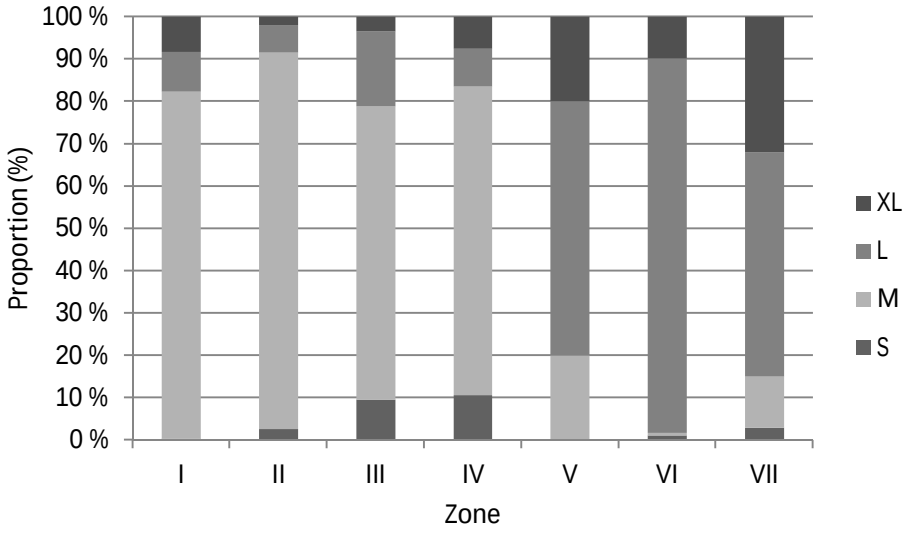

Figure 9. Proportions of different-sized species in each trapping zone. Small (S) species are less than 5 mm, medium-sized species (M) are 5-8 mm, large (L) species are 8-10 mm and very large (XL) species are more than 10 mm long (see Table 6.)

Table 9. Regression model explaining the proportion of beetles belonging to small and medium-sized (< 8 mm) species by connectivity (S_1), altitude and vegetation quality of the trapping transects. All transects are included in the model.

					95% Confidence Interval	
Parameter	B	Std. Error	t	Sig.	Lower Bound	Upper Bound
Intercept	0.29	0.099	2.9	0.005	0.088	0.49
S1	2,164E-005	3,721E-005	0.6	0.563	-5,306E-005	9,634E-005
Altitude	0.001	< 0.001	7.9	< 0.001	0.001	0.002
VegClass	-0.092	0.024	-3.8	< 0.001	-0.14	-0.043

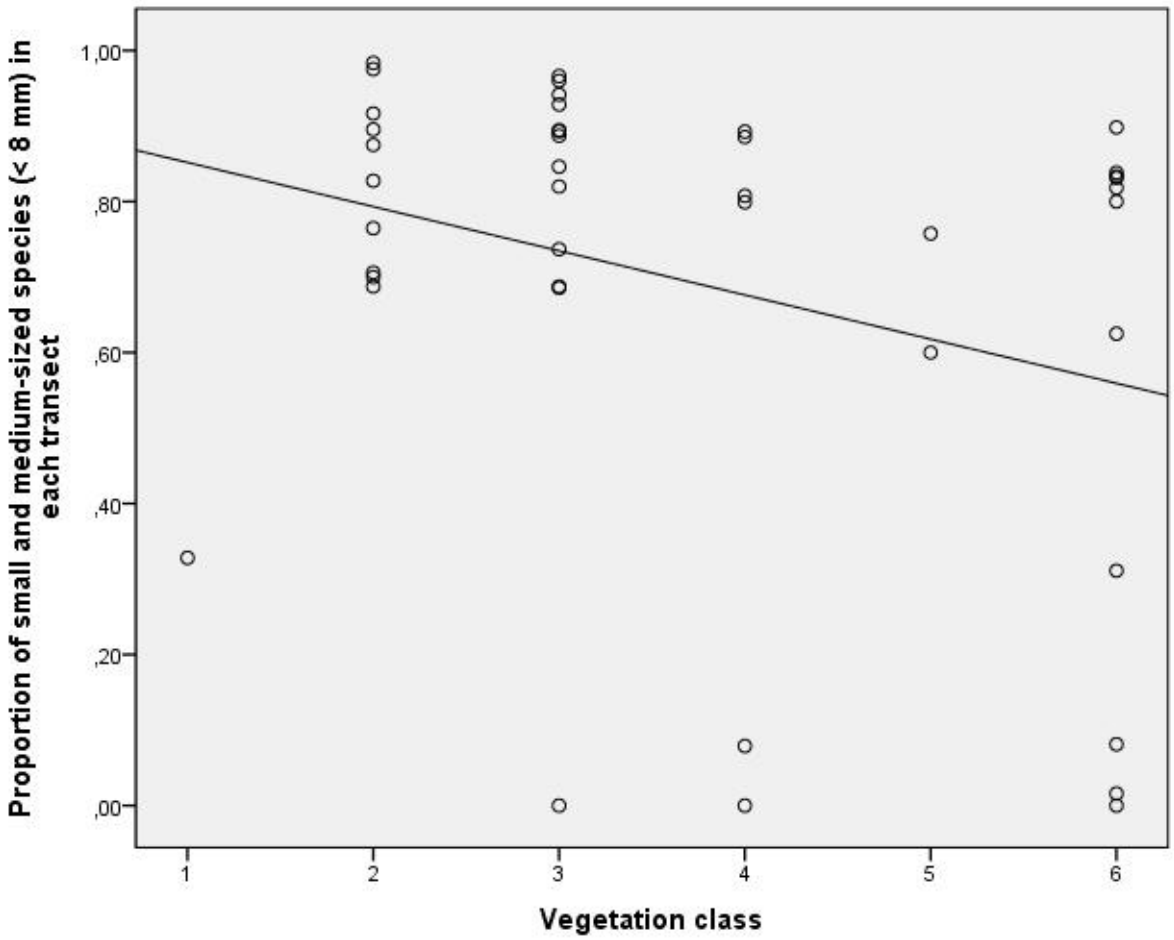

Figure 10. Relationship between the proportion of small and medium-sized species and vegetation class. Only transects with ten or more individuals collected are included.

4.5 Principal components analysis

Patterns in species assemblages (Table 10) and landscape variables (Table 11) were further analyzed with principal components analysis. In the case of species, PCA revealed similar patterns as the qualitative analysis presented above. The first three components explained together 56% of total variation. Oblimin rotation was performed to aid interpretation of the results (McGarical et al. 2000).

The first component is strongly correlated with *Nanos viettei, Epactoides major, Epilissus delphinensis, Apotolamprus helenae, Epilissus apotolamproides, Helictopleurus pseudofasciolatus* and somewhat more weakly with *Helictopleurus viridans*. This component corresponds to zones II to IV. The second component is correlated with *Helictopleurus rudicollis* and *Epactoides frontalis* and more weakly with *Nanos viettei*, and corresponds with zone I. The

third component is strongly correlated with *Epilissus prasinus*, *Nanos bimaculatus*, *Epilissus emmae obscurpennis* and *Helictopleurus viridans*. This component thus corresponds with zones VI and VII (Table 4).

Table 10. Correlations between the first three principal components and species abundances.

Variables	Component		
	1	2	3
% of total variation explained	25.9	15.8	14.4
Nanos viettei	0.786	0.428	
Epactoides major	0.762		
Epilissus delphinensis	0.748		
Apotolamprus helenae	0.683		
Epilissus apotolamproides	0.616		
Helictopleurus fasciolatus	0.605		
pseudofasciolatus			
Helictopleurus rudicollis		0.951	
Epactoides frontalis		0.932	
Apotolamprus quadrinotatus			
Helictopleurus viridiflavus			
Epilissus prasinus			0.815
Nanos bimaculatus			0.796
Epilissus emmae			0.731
obscurpennis			
Helictopleurus viridans	0.463		0.561

Landscape variables were subjected to PCA in order to reveal patterns in their relations to each other (Table 11). Only connectivity values for $\alpha = 1/30$ were included in order to reduce the number of strongly correlated variables. Four components were found with Eigenvalues more than one. All of them were chosen according to Catell's scree test. Oblimin rotation was performed to aid interpretation of the results (McGarical et al. 2000).

The first component consists of connectivities for the three forested vegetation types (primary forest, primary and secondary forests and primary, secondary and degraded forests) and vegetation density and quality. The second component includes connectivity for all vegetation types (primary, secondary and degraded forests and shrubbery) and altitude. The heights of the vegetation layers form the third component. The forth component consist of slope steepness

with a weak positive correlation to primary forest connectivity, and weak negative correlations between altitude and vegetation quality.

Table 11. Patterns among landscape variables revealed by principal components analysis. Values represent the Oblimin rotated correlations between components and original variables.

	Component			
	1	2	3	4
% of total variation explained	43.1	16.7	11.3	10.4
S_2 (α=1/30, P+S)	0.946			
S_3 (α=1/30, P+S+D)	0.938			
Tree density	0.840			
Vegetation class	0.791			-0.364
S_1 (α=1/30, P)	0.762			0.335
S_4 (α=1/30, ALL)		0.751		
Altitude		0.711		-0.507
Hight of veg. layer 3	0.478	-0.488	0.463	
Hight of veg. layer 1			0.929	
Hight of veg. layer 2			0.778	
Slope steepness				0.800

4.6 Effects of forest quality and fragmentation on dung beetles

As species number and abundance of Helictopleurini was low (Table 4), these analyses were restricted to Canthonini. The trapping effort varied between transects, which was taken into account by taking a residual from the regression of species number against the natural logarithm of sample size. The residuals describe differences in species richness arising from other causes than sample size.

At the level of the seven zones in Section 4.2, high positive residuals are located mainly in zones III (Ifanadiana), IV (Ambodihazo), VI (Sangasanga) and VII (Vatovavy), whereas in zones I (Talatakely), II (Kelilalina-Morafeno) and V (Morarano) the residuals are mainly negative (Fig. 11). These results are consistent, as expected, with the rarefaction results in Figure 8.

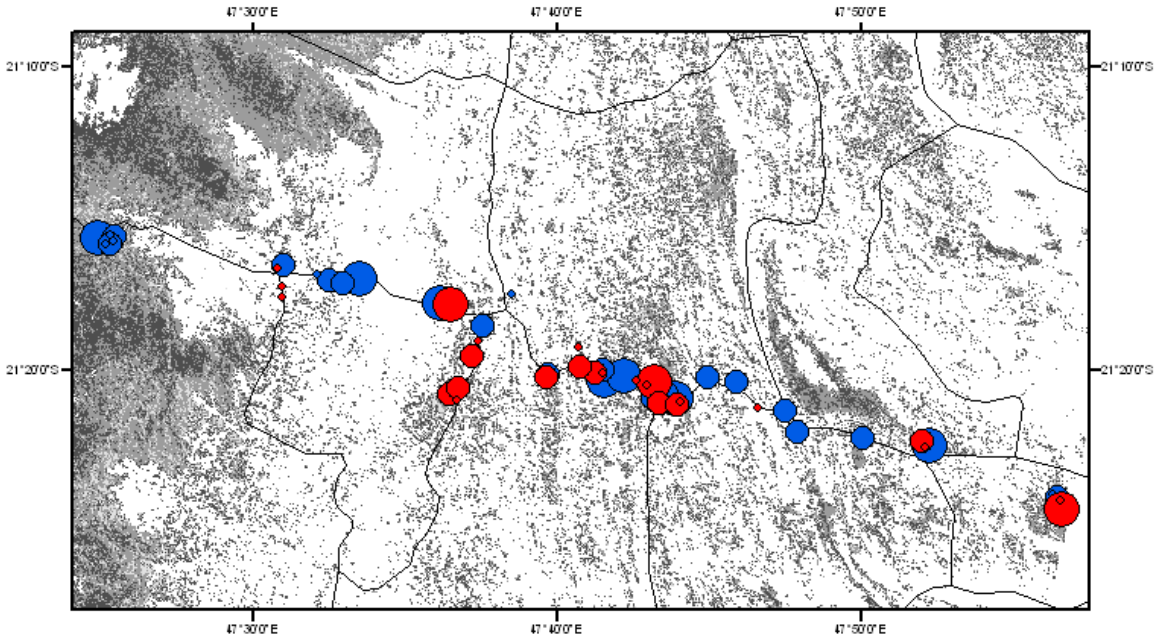

Figure 11. The circles show standardized residuals from the regression of the number of species against the natural logarithm of sample size in Canthonini. The size of the circle is proportional to the size of the residual. Red circles are positive and blue circles negative residuals.

As significant correlations were found between minimum temperature, vegetation class and altitude (see Section 4.1), I analyzed the combined effects of these and connectivity values on the residuals. Only transects in zones II–IV were included in the analysis as they were the best comparable ones due to their similar conditions. The correlation is highly significant for nearly all connectivity values (Table 12). Only connectivity values S_4, S_8 and S_{12}, which take shrubbery into account, show no correlation. A weak trend towards weaker correlation with smaller α can also be detected. The same analyses were repeated for zones VI and VII, which also form a homogenous area, but no significant correlations were found (Table 13).

Table 12. Correlations between the residuals and connectivity values in zones II–IV. Altitude and vegetation class (Table 1) are included in the model.

	F	*P*
α=1/30		
S_1 (P)	14.7	< 0.001
S_2 (P+S)	22.5	< 0.001
S_3 (P+S+D)	36.1	< 0.001
S_4 (P+S+D+SH)	3.3	0.082
α=1/100		
S_5 (P)	17.1	< 0.001
S_6 (P+S)	19.4	< 0.001
S_7 (P+S+D)	19.0	< 0.001
S_8 (P+S+D+SH)	2.8	0.109
α=1/500		
S_9 (P)	9.0	0.006
S_{10} (P+S)	7.7	0.010
S_{11} (P+S+D)	5.7	0.025
S_{12} (P+S+D+SH)	2.5	0.126

Table 13. Correlations between the standardized residuals and connectivity values in zones VI-VII. Altitude and vegetation class are included in the model.

	F	*P*
α=1/30		
S_1 (P)	0.013	0.915
S_2 (P+S)	0.040	0.854
S_3 (P+S+D)	0.034	0.865
S_4 (P+S+D+SH)	0.675	0.472
α=1/100		
S_5 (P)	0.373	0.595
S_6 (P+S)	0.024	0.887
S_7 (P+S+D)	0.687	0.468
S_8 (P+S+D+SH)	0.081	0.794
α=1/500		
S_9 (P)	1.655	0.289
S_{10} (P+S)	0.153	0.722
S_{11} (P+S+D)	1.355	0.329
S_{12} (P+S+D+SH)	3.609	0.154

The F- and *P*-values for the effect of vegetation class in the same analysis are presented in Table 14. Also vegetation class has significant effect on the residuals with several connectivity values. Vegetation class does not have significant effect on the residuals when shrubbery is included in the connectivity value (S_4 and S_8) or when α=1/500.

Table 14. Correlations between the residuals and vegetation class in zones II–IV. The model includes also connectivity and altitude, and it has been repeated with different connectivity values.

	F	*P*
α=1/30		
S_1 (P)	3.2	0.029
S_2 (P+S)	4.4	0.007
S_3 (P+S+D)	6.6	0.001
S_4 (P+S+D+SH)	1.7	0.182
α=1/100		
S_5 (P)	3.4	0.022
S_6 (P+S)	3.7	0.016
S_7 (P+S+D)	3.8	0.014
S_8 (P+S+D+SH)	1.6	0.195
α=1/500		
S_9 (P)	2.4	0.078
S_{10} (P+S)	2.1	0.110
S_{11} (P+S+D)	2.0	0.126
S_{12} (P+S+D+SH)	1.5	0.223

More detailed information about one of the analyses (with connectivity value S_1) is presented below (Table 15) and the correlation between connectivity (S_1) and the residuals is illustrated in Fig. 12.

Table 15. Analysis of variance for the combined effect of altitude, vegetation class and S1 (connectivity of primary forest, α=1/30) on species richness (the residuals).

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Intercept	0.1	1	0.1	0,2	0.623
Altitude	0.4	1	0.4	0.8	0.375
S_1	8.4	1	8.4	15.7	< 0.001
Vegetation class	6.8	4	1.7	3.2	0.029
Error	14.5	27	0.5		
Total	31.5	34			
Corrected Total	30.5	33			

Adjusted $R^2 = 0.42$

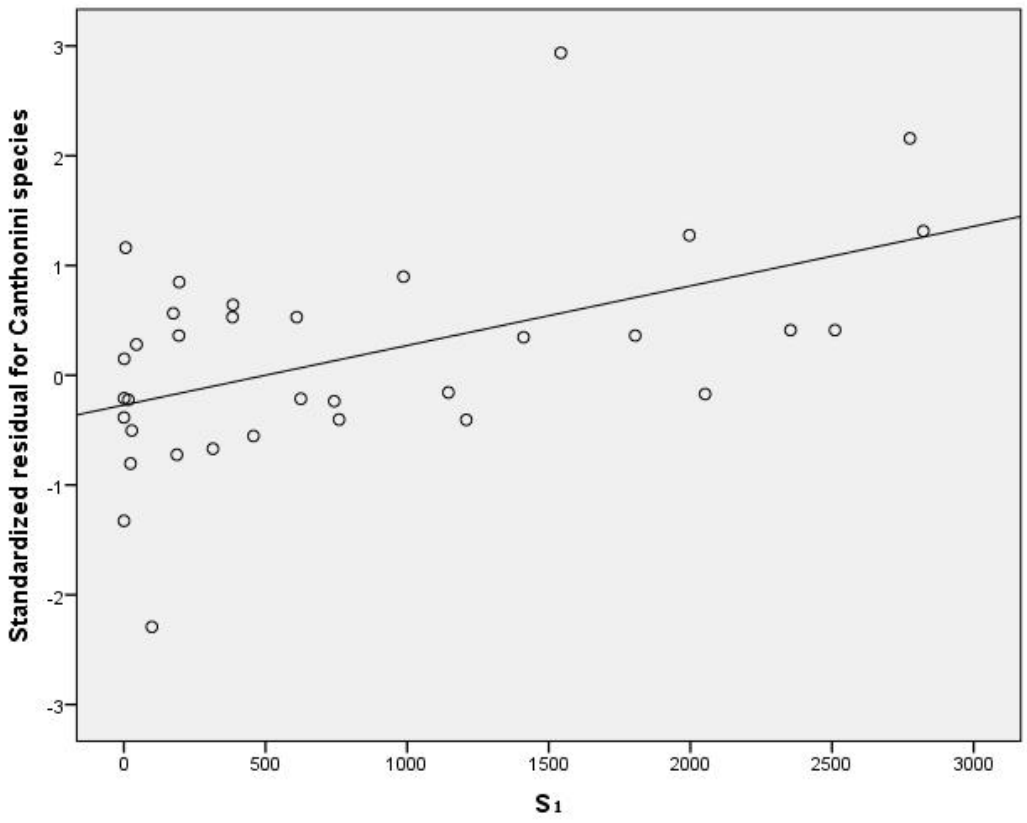

Figure 12. The correlation between the standardized residuals for Canthonini species in zones II–IV and connectivity (S_1).

5 Discussion

The aim of this study was to compare the structure of dung beetle communities between intensively modified landscapes on the east coast of Madagascar, east of the Ranomafana National Park, and areas of remaining primary rainforest. Two areas of primary rainforest were used for the comparison: Ranomafana National Park and the smaller area around the isolated Vatovavy mountain. The main result from this study is that the species assemblages in the forest fragments and degraded forest areas have surprisingly high species richness. Many species of dung beetles that are considered to be restricted to forests were sampled in small forest fragments. As expected, more species were present in areas where the original forest vegetation had been best preserved, but even low-quality fragments harbored many species.

Much of the lowland forest in eastern Madagascar was probably lost a long time ago, but records for the past 50 years demonstrate further extensive loss during this period (Knopp et al. 2011, Puhakka 2012). Given that much of the forest loss and fragmentation is relatively recent, there is the possibility that the populations within the fragmented forest landscape studied here have not yet reached an equilibrium with respect to the current amount of forest. In other words, the community in the fragmented landscape may have substantial extinction debt (Saunders et al. 1991, Hanski 2005). Therefore, the present results should not be interpreted as demonstrating that the fragmented and degraded forest landscapes will necessarily support viable populations of the species to the future.

In addition to the effects of forest loss and fragmentation, this study revealed interesting patterns in the occurrence of particular genera, especially *Epilissus* and *Nanos*. It has been shown before that four species of *Epilissus* inhabit different elevations in the Ranomafana National Park (Viljanen et al. 2010b). Two of them, *E. mantasoae* and *E. genieri*, occur at high elevations (mainly above 1000 m), while two others, *E. delphinensis* and *E. apotolamproides,* at lower elevations (mainly below 850 m) (Viljanen et al. 2010b). My results from Vatovavy area suggest that the same kind of pattern is present also at lower elevations, with *E. prasinus* and *E. emmae obscurpennis* being common at elevations below 300 m, and *Nanos bimaculatus* replacing the most common *Nanos* in the Ranomafana area, *N. viettei*, below 300 m.

Below, I will discuss in greater detail the reliability of the results (Section 5.1), the species composition of each genus in the study area (Section 5.2), and how forest loss and fragmentation affect dung beetle communities (Section 5.3).

5.1 The methods

The effects of rainforest loss and fragmentation on dung beetle communities have been studied elsewhere using similar methods. The trapping is usually done with dung- or carrion-baited pitfall traps. Variables describing forest loss and fragmentation have included forest fragment size, vegetation type (primary, secondary, plantation etc.), connectivity, isolation time and presence of mammals (e.g. Estrada et al. 1999). The features of dung beetle communities that have been studied include total species richness, species abundance distribution and community evenness (Nichols et al. 2007). In addition, the types of species that suffer the most and most rapidly from forest loss have been identified (Nichols et al. 2007, Slade et al. 2007, Barragán et al. 2011).

In many studies, vegetation type and connectivity have been characterized with very simplified classifications. Vegetation type has often been classified based on the type of modification rather than its effect on vegetation quality and microclimate. Distance to the nearest neighbouring fragment or continuous forest has been used to describe connectivity (Nichols et al. 2007). As microclimate has been concluded to be the most important environmental feature influencing dung beetle populations in a given area (e.g. Quintero and Halffter 2009), I attempted to classify the vegetation in the fragments according to its capability to sustain the original microclimatic conditions. Thus, my vegetation classification is based more on forest structure and canopy coverage than the type of modification. The weakness in my classification is subjectivity. On the other hand, the observer has been the same for all fragments, which means that the measures should be comparable across the fragments. Concerning connectivity, it has been observed that the distance to the nearest neighbouring fragment or continuous forest is not an accurate way to describe it (Hanski 2005). One approach to consider more features that affect dispersal rates among forest fragments is to calculate connectivity to all surrounding forest fragments and hence to all possible source populations. In the present study, I modified this approach to landscapes with continuous variation in forest quality (Section 3.2).

I used only carrion baits in this study, prepared of either fresh-water fish or chicken intestine. These bait types have been observed to attract generalists and carrion specialists equally well, but the dung specialists (about 20% of dung beetle species in the Ranomafana region) (Viljanen et al. 2010b) are necessarily left out of this study. This does not reduce the validity of the study, because the bait type does not vary between the sites. Nevertheless, the question remains whether dung specialists would respond in a different manner to forest loss and fragmentation compared to carrion feeders and generalists.

5.2 Dung beetle assemblages

Different groups of dung beetles have dissimilar ecologies, hence I will discuss below the results separately for the six genera of *Helictopleurus, Epilissus, Arachnodes, Nanos, Apotolamprus,* and *Epactoides*. *Helictopleurus* is the only genus in the endemic subtribe Helictopleurina, while the five other genera belong to the tribe Canthonini. The six genera represent four different evolutionary radiations, that is, the extant species originate from four independent colonizations of Madagascar (Wirta et al. 2008, Wirta et al. 2010, Miraldo et al. 2011), namely *Helictopleurus*, *Arachnodes-Epilissus*, *Nanos-Apotolamprus*, and *Epactoides*. The vast majority of species in all four radiations occur in wet forests in northern and eastern Madagascar (Miraldo et al. 2011).

5.2.1 Helictopleurina

I collected 5 species of *Helictopleurus*, of which *H. quadripunctatus* has shifted to use cattle dung and occurs in open and semiopen habitats across entire Madagascar (Rahagalala et al. 2009). Only one individual of this species was collected in a fragment of class 2 vegetation in zone V, although several fragments especially in zones 2 and 5 were really degraded and open and *H. quadripunctatus* has been observed to use also other resources than cattle dung (Wirta et al. 2008). The rest of the open habitat species are predominantly cattle dung specialists (Rahagalala et al. 2009, Miraldo et al. 2011), which likely explains their absence in my sample.

Helictopleurus rudicollis is a common and widely distributed species in wet forests in Madagascar with a generalist diet (Viljanen et al. 2010b). In the Ranomafana area it has been collected only at altitudes over 600 m asl, whereas in northern Madagascar is occurs also at lower elevations. In my samples it was found only in the continuous forest in the Ranomafana National Park.

Helictopleurus fasciolatus pseudofasciolatus is the only species that occurred across all the sampling sites. *Helictopleurus fasciolatus* is a generalist species with several subspecies and with a very wide distribution. Differences in elevational occurrence have been observed between the closely related species *H. fasciolatus* and *H. neuter* in northern Madagascar, where the former is more common in low elevations and the latter in mid-elevations (Viljanen et al. 2010b). In southeast and in the absence of *H. neuter* or any other similar species, *H. fasciolatus* occurs across a greater elevational gradient from sea level to as high as 1200 m asl (Metapopulation Research Group, dung beetle database 2013).

Helictopleurus viridans is a carrion specialist (Viljanen et al. 2010b) with a wide distribution extending from Andohahela National Park in southern Madagascar to Masoala and Marojejy in the north. It has been collected from a wide range of elevations from nearly sea level (Masoala) to as high as 950 m asl (Andasibe) (Metapopulation Reasearch Group, dung beetle database 2013). *Helictopleurus rudicollis* and *H. viridans* both have a wide distribution across wet forests in Madagascar, but they do not co-occur in the Ranomafana area. As *H. rudicollis* is only found in continuous forest in RNP, and *H. viridans* in the fragments, a question arises whether a carrion specialist (*H. viridans*) is more competitive in forest fragments where larger mammals like lemurs *Propithecus diadema edwardsi* and *Varecia variegata* are scarce (Gantzhorn et al. 2003). The resources produced by endemic mammals may have been partly replaced by those of invasive rodents like *Rattus rattus*, which have been observed to spread easily in many kinds of habitats including forest fragments (Gantzhorn et al. 2003). However, it remains unclear how well the tunneling Helictopleurini and other Malagasy dung beetles are able to utilize this new and different resource.

Finally, *Helictopleurus viridiflavus* is a small-sized species (5–7 mm) (Viljanen et al. 2010b), which I collected in small numbers exclusively in the fragments. It has been collected in the Ranomafana National Park in small numbers before, but it has been classified as a dung specialist (Viljanen et al. 2010b). With a few individuals sampled, generalizations about diets are uncertain. It is probable that *H. viridiflavus*, like many other species in the basal *Helictopleurus* clades, have a preference for dung (Wirta et al. 2008), but can also use other resources when dung is scarce. The species was sampled with dung baits in the Ranomafana National Park (Viljanen et al. 2010b), which supports a diverse community of lemurs and other dung-producing

mammals (Wright & Andriamihaja 2002), and with carrion baits in the fragmented area, where large mammals are scarce (Gantzhorn et al. 2003, Lehman et al. 2006, Irwin et al. 2010).

5.2.2 *Epilissus* and *Arachnodes*

The *Arachnodes* clade, including *Arachnodes, Epilissus* and *Apterepilissus*, represents along with Helictopleurini the oldest colonization of dung beetles to Madagascar (Miraldo et al. 2011). Five species of *Arachnodes* and four species of *Epilissus* were collected in my sampling.

All of the *Arachnodes* were collected from the fragments, and they were unidentifiable with the help of University of Helsinki collections. Based on the preliminary study in the Paris Museum of Natural History, at least two of these species may well be new to science (O. Montreuil, pers. comm.). Even though the dung beetle community in the fragmented area between Ranomafana and Vatovavy has not been studied before, it is surprising that new species were found within a small area, near the intensively sampled Ranomafana National Park and with relatively little effort. It is possible that these species represent lowland species that do not occur in the Ranomafana National Park. Thus it is possible that forest fragments in areas with high degree of human impact have been able to retain species lacking from conservation areas. Most remaining primary rainforest in Madagascar is located on mountain slopes at higher elevations, and most lowland rainforest has been converted to agricultural purposes (Green & Sussmann 1990, Vågen 2006).

Epilissus delphinensis and *E. apotolamproides* are among the most common species in the Ranomafana National Park, where they have been observed to exhibit elevational differentiation with two high elevation species, *E. mantasoae* and *E. genieri* (Viljanen et al. 2010b). Interestingly, these two species pairs consist of species of different sizes, with *E. delphinensis* and *E. mantasoae* being large, and *E. apotolamproides* and *E. genieri* being small (Viljanen et al. 2010b). In my sample, *E. apotolamproides* and *E. delphinensis* were found in all zones at elevations between 97–1014 m asl and 298–1014 m asl, respectively. In addition to them, two large species, *Epilissus prasinus* and *Epilissus emmae obscurpennis*, were collected in Vatovavy and Sangasanga. They both occurred at elevations of 135–459 m asl. Even though these species pairs have overlapping occurrences, the vast majority of both *E. apotolamproides* and *E.*

delphinensis occur above 400 m asl, which suggests elevational divergence in *Epilissus* also at low altitudes.

5.2.3 *Nanos* and *Apotolamprus*

The *Nanos* clade has been ecologically very successful, and many species in the genera *Nanos* and *Apotolamprus* are among the most common species in nearly all local communities in wet forests in Madagascar (Viljanen 2009). The same applies to my sample, as *Apotolamprus helenae* and *Nanos viettei* were clearly the most abundant species in zones I to IV, and *Nanos bimaculatus* was the most abundant one in zones VI and VII. In addition to these species, my sample included A*potolamprus quadrinotatus, A. manomboensis* and an unidentified *Nanos* cf. group *minutus*.

There is a similar elevational differentiation in *Nanos* than in *Epilissus*. *Nanos bimaculatus* completely replaces *N. viettei* at elevations below 450 m asl and therefore *N. bimaculatus* is the dominant species from Morarano to east, and the most dominant species in Ranomafana, *N. viettei*, was only found at higher elevations at the Vatovavy mountain.

In previous studies, the same kind of differentiation has been observed between *Apotolamprus quadrinotatus* and *A. helenae*, with the former species being more common above 800 m asl and the latter one being dominant below that elevation (Viljanen et al. 2010b). My sample of *A. helenae* fits well with these previous results, as the vast majority of the individials were collected below 650 m asl, and only 4 above 900 m asl. On the other hand, *A. quadrinotatus* was collected at way lower elevations than expected, at 468-981 m asl, with most individuals sampled from Ambodihazo (zone IV) at altitudes around 500 m asl. These results pose the question whether *A. quadrinotatus* is able to inhabit this area due to relaxed competition with larger species or because habitat loss has forced the species to move to less suitable areas.

Apotolamprus manomboensis is a small-bodied generalist species originally found from Manombo on the east coast, but it has been lately recognised to be more widely distributed and to occur also in Ranomafana (H. Viljanen, pers. comm.). Only one individual of this species was collected.

5.2.4 *Epactoides*

The fourth succesfull radiation of Malagasy dung beetles is represented by *Epactoides*, most of which are small-bodied, uncommon and often inhabit marginal ecological conditions (Miraldo et al. 2011). Four species of *Epactoides* were included in my sample: *E. frontalis*, *E. mahaboi*, *E. major* and *E. tiinae*. All species were found from different locations: *E. frontalis* from Talatakely, *E. major* from the fragments, *E. mahaboi* from Sangasanga and *E. tiinae* from Vatovavy, which suggests that there might be some elevational differentiation in *Epactoides*. *Epactoides major* was clearly the most abundant species in my samples and among the six most common species in the fragments (zones 2–4).

5.3 Effects of forest loss and fragmentation on dung beetle community

The dung beetle community in the Ranomafana National Park, and especially Talatakely area, is well known from previous studies (e.g. Viljanen 2010a). My sample from Talatakely in the continuous forest in the Ranomafana NP was clearly insufficient to include most of the species that are known to occur in this area (Table 5), but as the trapping effort and bait type were similar in all study areas the present results allow a fair comparison between the continuous and fragmented forest areas. Comparison with previous studies reveals that the species known from Talatakely but lacking from my sample are mostly either dung specialists, collected with tree traps, uncommon species or inhabit different elevations (Viljanen 2010a). Thus, my sample appears to include relatively well all the common generalist species in Talatakely. In addition, one unidentified *Nanos* (*N*. cf. group *minutus*) was collected, which suggests that new species can still be found in the area despite of its intensive sampling history.

Concerning the occurrence of the different-sized species in the study area, it can be concluded that the forest fragments of poor vegetation quality had larger proportion of small-sized species (Section 4.4). Except for the few very common species that the fragments (zones II to IV) share with Talatakely and Vatovavy (*Helictopleurus fasciolatus*, *H. viridans*, *Epilissus apotolamproides* and *E. delphinensis*) all species in the fragments were less than 8 mm in body length. Several small-bodied species were also much more abundant in the fragments than in areas of primary forest, including *Apotolamprus helenae*, *A. quadrinotatus* and *Epactoides major*. This result is similar to the conclusions of previous studies (e.g. Nichols et al. 2007, Slade et al. 2007).

Small species may utilize the dung and carcasses of small mammals and possibly also invertebrates (e.g. centipeds), many of which can be expected to be common in forest fragments. In any case it was surprising to find specimens of previously unknown species. The probable reason why these species have not been collected in the well-studied Ranomafana NP is elevation; the undescribed species of *Arachnodes* (*A*. ARARANO11A and *A*. ARARANO11B) were sampled at 448 to 538 m above sea level, while the lowest levels in the Ranomafana NP are around 600 m asl. These species may represent the possibly large number of lowland species that are now declining to extinction due to loss of habitat. An extreme example is provided by the completely isolated, 5000 ha fragment of lowland forest in Manombo on the east coast, from were no less than 8 species new to science were collected during a few days of sampling in 2004 (Montreuil & Viljanen 2007, Montreuil 2005, Montreuil 2006, Montreuil 2008).

Altogether, more species were found from the fragments than from Talatakely. This is at least partly due to greater pooled trapping effort and wider variation of habitat types in the fragments, but the result also suggests that forest remnants and secondary vegetation may have an important role in biodiversity conservation. On the other hand, there were so many small and low-quality fragments with surprisingly high species diversity that some degree of extinction debt is likely to be present. If no reforestation takes place, these populations and species will eventually go extinct (Hanski 2005, Saunders et al. 1991).

According to the statistical analyses there are more species of Canthonini in better connected forest fragments with better vegetation quality. Significant positive correlations between Canthonini richness and connectivity were found in all cases when connectivity had been calculated for the forested vegetation types. At the same time, the correlations between Canthonini species richness and connectivity of all vegetation types were never significant. Vegetation quality also had significant effect on Canthonini species richness in several cases. According to these results, connectivity of forested vegetation types and forest quality are very important for Canthonini communities. This assumption is consistent with the results of the principal component analysis (Table 6), which places S_4 into a different component than the other connectivity measures. These results fit well with previous studies, which have concluded that forest quality and microclimate are the main factors influencing the diversity of forest dwelling dung beetles (Nichols et al. 2007, Navarrete & Halffter 2008, Quintero & Halffter 2009).

It is easy to understand that a diverse dung beetle community cannot persist in a fragment consisting mainly of shrubbery, no matter how well connected it is.

Forest-dwelling dung beetles have strict microclimatic requirements (Sheldon et al. 2011, Välitalo 20102). As the conditions between rainforest and open habitats are very different, dung beetle communities in these two habitat types usually consist of completely different species. The situation is the same in Madagascar, where the number of dung beetles that thrive in open habitats is small. This is due to the dominance of forest habitats in the past, and the small number of introduced open habitat species (Wirta et al. 2008, Rahagalala et al. 2009, Miraldo et al. 2011). My results suggest that, like elsewhere in the tropics, forest fragmentation and degradation reduce dung beetle species diversity also in Madagascar. Moreover, small-bodied species dominate the communities in the remaining fragments. This may have consequences for ecosystem functioning, as the small-bodied species are not able to compensate for the loss of large ones in functions like nutrient cycling, bioturbation and secondary seed dispersal (Didham et al. 1996, Slade et al. 2007, Slade et al. 2010, Barragán et al. 2011). Rainforest degradation may thus reduce forest regeneration via reduced capacity of dung beetle species.

6 Conclusions

Like elsewhere in the tropics, the forest-dwelling dung beetle community in Madagascar is affected by habitat degradation and fragmentation. Well-connected areas of high quality vegetation can sustain more species than areas where anthropogenic modification has been more intense. Even though there are unexpectedly species-rich dung beetle communities also in small and isolated fragments, those communities are typically dominated by small-bodied species. The disappearance of large species is of concern as they have been shown to be especially important in providing ecosystem services like nutrient cycling and seed dispersal (Didham et al. 1996, Slade et al. 2007, Slade et al. 2010, Barragán et al. 2011). In areas with little or no forested vegetation, no forest-dwelling species can survive.

During the intensive research on the ecology and biogeography of Malagasy dung beetles, researchers from the University of Helsinki have found several groups of species in which different species with similar ecologies occur at different elevations (Viljanen et al. 2010b). My study reveals two more cases where the occurrences of ecologically similar species are

elevationally differentiated. This result and the previously unknown species found from the fragments between Ranomafana and Vatovavy suggest that the Malagasy dung beetle communities have been even more diverse than previously thought before the lowland forests were cleared. Even though the last representatives of these lowland species can still be found in the small forest refugia that remain in low altitudes, their possibilities to survive in the long term are small in unprotected fragments located in areas with great human pressure on land use.

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Appendices

Appendix 1. Location, trapping period, coordinates and altitude of the study transects.

Transect	Location	Trapping period	Latitude	Longitude	Altitude (m)
1	Morafeno	18.-20.11.2011	21° 16' 39,9''	47° 30' 49,6''	599
2	Madiorano	18.-20.11.2011	21° 16' 33,1''	47° 31' 00,0''	616
3	Tsaratango	19.-21.11.2011	21° 16' 52,3''	47° 32' 05,9''	637
4	Manoqaqora	19.-21.11.2011	21° 17' 02,3''	47° 32' 30,4''	620
5	Manoqaqora	21.-23.11.2011	21° 17' 07,7''	47° 32' 58,5''	637
6	Kelilalina	21.-23.11.2011	21° 17' 01,3''	47° 33' 30,6''	624
7	Andranofolahana	24.-26.11.2011	21° 17' 47,5''	47° 36' 10,5''	544
8	Alamaitso	24.-26.11.2011	21° 17' 52,3''	47° 36' 29,6''	510
9	Ifanadiana	24.-26.11.2011	21° 18' 33,2''	47° 37' 34,5''	470
10	Ifanadiana	25.-27.11.2011	21° 19' 32,4''	47° 37' 11,7''	448
11	Ifanadiana	25.-27.11.2011	21° 19' 04,1''	47° 37' 23,4''	486
12	Talatakely	28.-30.11.2011	21° 15' 51,5''	47° 25' 08,7''	965
13	Talatakely	28.-29.11.2011	21° 15' 35,5''	47° 25' 26,6''	981
14	Talatakely	28.-30.11.2011	21° 15' 40,5''	47° 24' 54,0''	903
15	Talatakely	29.11.-1.12.2011	21° 15' 45,6''	47° 25' 25,4''	978
16	Talatakely	29.11.-1.12.2011	21° 15' 51,5''	47° 25' 17,8''	1014
17	Antanambao	1.-3.12.2.2011	21° 19' 53,6''	47° 40' 43,9''	572
18	Antanifotsy	1.-3.12.2.2011	21° 17' 31,5''	47°38' 29,5''	411
19	Talatakely	1.-3.12.2.2011	21° 15' 32,0''	47° 25' 17,2''	920
20	Ambodirafia	6.-8.12.2011	21° 20' 21,5''	47° 41' 32,1''	522
21	Ambodihazo	6.-8.12.2011	21° 20' 24,6''	47° 43' 11,5''	512
22	Andranomangatsiaka	9.-10.12.2011	21° 20' 55,3''	47° 34' 26,6''	517
23	Masoarivo	9.-10.12.2011	21° 21' 03,5''	47° 44' 02,0''	538
24	Vatovavy	12.-14.12.2011	21° 24' 18,8''	47° 56' 32,9''	298
25	Vatovavy	12.-14.12.2011	21° 24' 36,8''	47° 56' 37,6''	459
26	Vatovavy	12.-14.12.2011	21° 24' 27,3''	47° 56' 20,1''	453
27	Vatovavy	13.-15.12.2011	21° 24' 06,2''	47° 56' 17,9''	176
28	Vatovavy	13.-15.12.2011	21° 24' 11,1''	47° 56' 27,4''	215
29	Sangasanga	16.-18.12.2011	21° 22' 29,9''	47° 52' 13,9''	135
30	Sangasanga	16.-18.12.2011	21° 22' 33,9''	47° 52' 06,9''	97
31	Sangasanga	17.-19.12.2011	21° 22' 21,7''	47° 51' 59,0''	206
32	Tsaramasoandro	21.-23.12.2011	21° 20' 36,7''	47° 36' 45,3''	465
33	Tsaramasoandro	21.-23.12.2011	21° 20' 49,5''	47° 36' 27,2''	508
34	Tsaramasoandro	21.-23.12.2011	21° 20' 58,9''	47° 36' 41,5''	497
35	Ampasipotsy	22.-24.12.2011	21° 17' 35,0''	47° 30' 58,3''	632
36	Ampasipotsy	22.-24.12.2011	21° 17' 15,8''	47° 30' 56,3''	615
37	Antanambao	26.-28.12.2011	21° 20' 06,0''	47° 41' 14,0''	498
38	Antanambao	26.-28.12.2011	21° 19' 59,0''	47° 41' 31,6''	515
39	Antanambao	26.-28.12.2011	21° 20' 07,3''	47° 41' 30,8''	516
40	E of Ifanadiana	27.-29.12.2011	21° 20' 16,6''	47° 39' 39,1''	509
41	W of Antanambao	27.-29.12.2011	21° 21' 01,2''	47° 39' 46,2''	532
42	E of Ifanadiana	27.-29.12.2011	21° 20' 09,6''	47° 39' 42,5''	516
43	W of Kianjavato	30.12.2011-2.1.2012	21° 22' 14,5''	47° 50' 03,1''	114
44	W of Kianjavato	30.12.2011-2.1.2012	21° 22'01,8''	47° 47' 53,3''	174
45	W of Kianjavato	30.12.2011-2.1.2012	21° 20' 23,6''	47° 45' 53.0''	292
46	Ambodihazo	3.-5.1.2012	21° 20' 10,9''	47° 42' 11,5''	479
47	Ambodihazo	3.-5.1.2012	21° 21' 07,2''	47° 43' 22,5''	491
48	Ambodihazo	4.-6.1.2012	21° 20' 56,5''	47° 43' 08,8''	471
49	Ambongo	4.-6.1.2012	21° 21' 08,9''	47° 43' 56,8''	533
50	Ambongo	4.-6.1.2012	21° 20' 56,8''	47° 43' 54,6''	527
51	Morarano	8.-10.1.2012	21° 21' 22,2''	47° 47' 30,3''	207
52	Morarano	8.-10.1.2012	21° 21' 15,8''	47° 46' 36,5''	237
53	E of Ambongo	8.-10.1.2012	21° 20' 16,6''	47° 44' 58,1''	367
54	Ambodihazo	9.-11.1.2012	21° 20' 29,2''	47° 42' 58,7''	468
55	Ambodirafia	9.-11.1.2012	21° 20' 20,3''	47° 42' 35,0''	488

Appendix 2. Numbers of individuals collected in transects in zones 1-3 (transects 1–16, 18, 19 and 32–36).

Location	Talatakely	Talatakely	Talatakely	Talatakely	Talatakely	Talatakely	Morafeno	Ampasipotsy	Ampasipotsy	Madiorano	Tsaratango	Manoqaqora	Manoqaqora	Kelilalina	Andranofolahana	Alamaitso	Tsaramasoandro	Tsaramasoandro	Tsaramasoandro	Ifanadiana	Ifanadiana	Ifanadiana	Antanifotsy
Order from west	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Transect	14	12	16	19	15	13	1	35	36	2	3	4	5	6	7	8	33	34	32	10	11	9	18
Apotolamprus helenae (Montreuil, 2004)	2		2					36	19	22		30	7	1	6	10	49	19	7	3	16		21
Apotolamprus manomboensis (Montreuil, 2006)								1															
Apotolamprus quadrinotatus (Boucomont, 1937)						1											5						
Arachnodes ARARANO11																3	2			2			
Arachnodes ARARANO11b									1														
Arachnodes ARARANO11c																1							
Arachnodes ARARANO11d																							
Epactoides frontalis (Montreuil, 2003)			1																				
Epactoides mahaboi (Paulian, 1976)																							
Epactoides major (Paulian, 1991)								2	18							4	29	12	5		4		
Epactoides tiinae (Montreuil, 2005)																							
Epilissus apotolamproides (Lebis, 1961)	5	1	5		5			10		1		7				2	11	3	1		1		9
Epilissus delphinensis (Lebis, 1953)	4	5	22	13	13	7		7	1			5	1		1	2	13	6	1				
Epilissus emmae obscurpennis (Montreuil, 2006)																							
Epilissus prasinus (Klug, 1832)																							
Helictopleurus pseudofasciolatus (Fairmaire, 1898)	1		13	9	4	3		12	1	2	7	8	1	1	2	1	13	11	8	1	2		34
Helictopleurus quadripunctatus (Olivier, 1789)																							
Helictopleurus rudicollis (Fairmaire, 1898)	1	2	19	2	2	1																	
Helictopleurus viridans (Fairmaire, 1901)															1	3	9					5	
Helictopleurus viridiflavus (Fairmaire, 1898)									1			2											
Nanos bimaculatus (Künckel, 1887)																							
Nanos NANORANO11						1											3			1			
Nanos viettei (Paulian, 1976)	55	36	288	40	120	95	1	185	81	50	113	59	50	10		7	273	25	10		5		

Appendix 3. Numbers of individuals collected in transects in zones 4-7 (transects 17, 20–31 and 37–55).

Location	E of Ifanadiana	E of Ifanadiana	W of Antanambao	Antanambao	Antanambao	Antanambao	Antanambao	Ambodirafia	Ambodihazo	Ambodirafia	Ambodihazo	Ambodihazo	Ambodihazo	Ambodihazo	Andranomangatsiaka	Ambongo	Ambongo	Masoarivo	E of Ambongo	W of Kianjavato	Morarano	Morarano	W of Kianjavato	W of Kianjavato	Sangasanga	Sangasanga	Sangasanga	Vatovavy	Vatovavy	Vatovavy	Vatovavy	Vatovavy
Order from west	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55
Transect	40	42	41	17	37	38	39	20	46	55	54	48	21	47	22	50	49	23	53	45	52	51	44	43	31	30	29	27	26	28	24	25
Apotolamprus helenae (Montreuil, 2004)	3	4	6	9	7	61	28	46	11	18	32	51	11	20	4	76	7	5			1				1							
Apotolamprus manomboensis (Montreuil, 2006)																																
Apotolamprus quadrinotatus (Boucomont, 1937)	1		2			5		3			18		35	3																		
Arachnodes ARARANO11										3		4		1				1														
Arachnodes ARARANO11b													1																			
Arachnodes ARARANO11c											1						1															
Arachnodes ARARANO11d					1								2																			
Epactoides frontalis (Montreuil, 2003)																																
Epactoides mahaboi (Paulian, 1976)																									2							
Epactoides major (Paulian, 1991)		2	7	1	5	11	1	2	9				7	18	1	15	16														3	2
Epactoides tiinae (Montreuil, 2005)																														1		
Epilissus apotolamproides (Lebis, 1961)	2	6	7	3	4	1	3		2	1	1		2	3		4	8								7	1					2	4
Epilissus delphinensis (Lebis, 1953)			1			33	2		15			8	2	23		30	2													10	6
Epilissus emmae obscurpennis (Montreuil, 2006)																									4		7	3				2
Epilissus prasinus (Klug, 1832)																									4		3	44	6	10	8	1
Helictopleurus pseudofasciolatus (Fairmaire, 1898)				1	2		5	2	25	3	4	2	3	19		9	1	2				3			1	2	1	1			2	1
Helictopleurus quadripunctatus (Olivier, 1789)																				1												
Helictopleurus rudicollis (Fairmaire, 1898)																																
Helictopleurus viridans (Fairmaire, 1901)						1			3	6	2																	7			2	
Helictopleurus viridiflavus (Fairmaire, 1898)													1																			
Nanos bimaculatus (Künckel, 1887)																									19	68	63	51		52	10	17
Nanos NANORANO11													1																			2
Nanos viettei (Paulian, 1976)	1	36	53	3	1	214	19	28	169	3	40		2	57		80													24			10